Productivity and population trends of northern lapwing (Vanellus vanellus) in Britain

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Summary

Northern Lapwing *Vanellus vanellus* have undergone recent declines in breeding numbers throughout Britain and Europe. These declines have been attributed to a reduction in productivity caused by a suite of changes in modern agricultural practice. First, whether management successfully slowed or reversed the downward trend in Northern Lapwing breeding numbers in Wales was assessed. Using data from a range of sites across Wales I asked whether management aimed specifically at Northern Lapwings significantly improved breeding densities or the number of fledged chicks. Management failed to improve either Northern Lapwing breeding densities or productivity. Second, fieldwork at four sites in North Wales in 2003 and 2004 was conducted. The aim was to: (i) test three different systems of remote digital camera designed to identify nest predators, (ii) assess what factors influenced Northern Lapwing habitat selection and nest survival, and (iii) assess what factors influenced chick growth rate, body condition and survival. A passive infra-red digital nest camera reliably identified nest predators whilst reducing power requirements. Predation was identified as the main cause of both nest failure and chick mortality, and mammalian predators were the most common nest predators. Chicks were generally in poor condition and chick predation rates were high. Evidence suggested that whilst predation was the proximate cause of chick mortality, starvation may have been the ultimate cause. Third, I investigated whether UK regional variation in Northern Lapwing population declines could be explained by variation in demographic parameters. It was not possible to explain these regional variations through source-sink dynamics, clutch failure rates or adult/first-year survival rates In conclusion, my work suggests it is likely that chick mortality is a main determinant of poor Northern Lapwing productivity and recent population declines. However, the determinants of chick mortality and predation rates are still poorly understood and further research is needed.

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Contents

Chapter 1.

Productivity and Population Trends of Northern Lapwings (*Vanellus vanellus*) in Britain

Fiona Sharpe

Introduction

Bird population trends, and the various factors that influence bird numbers are of fundamental interest to ecologists and those involved in the management of bird populations. The diurnal nature of most species of birds makes it easier to distinguish between species and lends itself to their popularity for observing and studying. Birds are regarded as good general indicators of biodiversity, the state of the environment and the sustainability of human activities as they are wide ranging in habitat distribution, and tend to be at or near the top of the food chain (Furness & Greenwood 1993). Consequently, the population ecology of birds is perhaps better known than that of any other group of organisms (Newton 1998).

Across Europe, the populations of many farmland bird species declined during the last quarter of the twentieth century, indicating severe damage to the continent's biodiversity (Donald *et al.* 2002). Modern agriculture should be regarded as a major anthropogenic threat to biodiversity, and agricultural intensification has been implicated in the recent severe declines in numbers and range in farmland bird populations across large parts of the continent (Fuller *et al.* 1995; Donald *et al.* 2000; Donald *et al.* 2002). Farmland bird population declines have been particularly severe in European Union (EU) member state countries where the Common Agricultural Policy has driven agricultural intensification, and therefore bird population declines, at a more rapid rate than state support for agriculture in eastern Europe (Pain & Pienkowski 1997; Donald *et al.* 2002).

The objectives of my PhD were to investigate the causes of population decline in a farmland indicator species the Northern Lapwing (*Vanellus vanellus*) and the implications for conservation initiatives.

Specifically, I asked:

- *What are the influences of nest survival and chick survival in determining productivity, and are current levels of productivity capable of maintaining a stable breeding population?*

- *What are the main causes of Northern Lapwing nest failure and chick mortality?*
- *Can regional variations in Northern Lapwing population declines within the United Kingdom be explained by variations in demographic parameters?*
- *To what extent have conservation initiatives aimed at slowing or reversing Northern Lapwing population declines in Wales been successful?*

For this work I used a combination of data from my own fieldwork in North Wales and UK-wide long term datasets. First I discuss the ecology of Northern Lapwings and the background into recent population declines. Then I discuss the specific objectives and main findings of each chapter. Finally I examine the implications of these results for conservation initiatives, and the potential avenues for future research of Northern Lapwing and other farmland bird population declines.

The Northern Lapwing

The Northern Lapwing belongs to a distinct group of birds known as shorebirds (waders), which includes sandpipers and their allies (superfamily Scolopacoidea) and plovers (superfamily Charadroidea). It is the most northerly distributed of the 24 species that make up the genus *Vanellus*, with the rest being found in tropical and sub-tropical areas. Northern Lapwings are largely terrestrial, inhabiting large, open habitats throughout Britain and Europe. As humans have been modifying the landscape for centuries, Northern Lapwings have become increasingly associated with farmland throughout their annual cycle (Hudson *et al.* 1994), and they occupy a wide variety of habitats ranging from natural sites such as fens, marshes and other wetlands, low heath, moorland and upland grasslands to agricultural grassland and arable crops. Throughout the breeding season Northern Lapwings are widely distributed across the temperate zone in Eurasia from 40 to 60 degrees north, although in Europe they may nest further north than this. In Britain, Northern Lapwings normally nest below an altitude of 500m, but they are not infrequent up to 800m, and they tend to winter at lower elevations (Cramp & Simmons 1983).

Ecology of Northern Lapwings

For most of the year, Northern Lapwings form large flocks moving from field to field feeding on predominantly soil and surface-living invertebrates, for example, earthworms and beetles. Northern Lapwings are visual hunters and therefore require access to the soil surface to find their prey items.

From early February onwards adults start to return in flocks from their winter-feeding grounds to suitable nest sites. Males return to nest sites before females, and soon establish territories about 0.25 – 2 ha in open habitat with short vegetation (Galbraith 1989a). Northern Lapwings tend to choose nest sites close to rivers or flooded areas and away from trees, bushes or other perches (Galbraith 1989a; Berg *et al.* 1992). Sites with relatively short, heterogeneous swards are also preferred for nesting, with the highest breeding density at vegetation heights of 10-15 cm (Shrubb & Lack 1991).

The breeding season normally lasts from mid-March to early July. Northern Lapwings were traditionally regarded as a monogamous species (Cramp & Simmons 1983), however recent studies have revealed a relatively high incidence of polygyny (Parish *et al.* 1997; Liker & Székely 1999, Lislevand 2003). Eggs are laid between late March and late May (Galbraith 1988a) and the normal clutch size is four eggs which are laid in grass-lined scrapes on the ground. To compensate for nest failure, Northern Lapwings are capable of relaying up to four replacement clutches (Cramp & Simmons 1983). Incubation period is normally 26 days after clutch completion (Larsen *et al.* 2003; Lislevand *et al.* 2004). Throughout the incubation period both adults share incubation, although females spend more time incubating and males spend more time on nest defence (Liker & Székely 1999).

Northern Lapwing chicks are nidifugous and precocial, and they hatch with well-developed legs but poorly-developed wings (Galbraith 1988b). They are capable of self-feeding and usually leave the nest within 12 hours of hatching. Usually both adults stay with the chicks (Liker & Székely 1999), brood them and guard them from predators. Broods are usually led to suitable feeding grounds. Chicks tend to feed opportunistically on both soil and surface-living invertebrates which they hunt for

visually (Galbraith 1989b). The chicks will then normally remain there until they fledge about 35 days after hatching (Galbraith 1988b).

Population Trends

Northern Lapwings were formally widespread across Britain and Europe, being a familiar bird on farmland. However, in recent decades, this terrestrial plover has experienced difficulties and they have declined within or disappeared from many lowland areas (Hudson *et al.* 1994). These declines are linked with recent changes in agriculture (Chamberlain *et al.* 2000a). Northern Lapwings are not the only farmland bird to have suffered population changes and range contractions. Other farmland birds, including the Tree Sparrow *Passer montanus*, Skylark *Alauda arvensis*, Corn Bunting *Miliaria calandra*, and Blackbird *Turdus merula* have all declined in numbers over a similar time period, and various studies have investigated the link between population decline and agricultural change (Fuller *et al.* 1995; Browne *et al.* 2000; Chamberlain & Siriwardena 2000; Chamberlain *et al.* 2000a; Chamberlain *et al.* 2000b; Gates & Donald 2000; Chamberlain & Fuller 2001; Robinson *et al.* 2001).

During the first half of the 20th century, Northern Lapwing numbers were influenced by several factors. A period of temporary climatic warming enabled Northern Lapwings to colonise northern Scotland, the Faeroes and northwards into Scandinavia and the USSR. Declines in many areas of temperate Europe were attributed to habitat loss and egg collecting (Hudson *et al.* 1994). In Britain, the decline at the start of the century was temporarily halted by the 1926 Lapwing act implementing protective measures against egg collection. The first large-scale survey of Northern Lapwings, carried out in Britain in 1937-38, was directed at habitat selection and no attempt was made to review numbers or status. Fisher (1941) made the first estimate of the size of the Northern Lapwing breeding population in Britain giving a figure of 175,000 pairs.

After the Second World War, the modern agricultural revolution took place. Farming intensified with a loss of grassland, and an increase in the area of land in tillage, as well as intensification in drainage, reseeding and the use of chemicals (Shrubb 1990; Peach *et al.* 1994). Population trends documented through the British Trust for

Ornithology (BTO)/Joint Nature Conservation Committee (JNCC) Common Bird Census (CBC) have revealed a steady decline since the 1950's, although the CBC trend for the 30 year period 1968-1998 shows relative stability until the early 1980's (Wilson *et al.* 2001). Since then there has been a steep and sustained population decline in the last 20 years (Wilson *et al.* 2001; Wilson *et al.* 2005). This decline has been most marked in southern England (Cramp & Simmons 1983). The decline in Northern Lapwing numbers over recent decades has not been restricted to Britain but is occurring throughout most of Europe and particularly in the European Union (Trolliet 2003; BirdLife International 2004). In Britain declines have been greatest in southwest England and Wales, and less severe in north England and Scotland (Wilson *et al.* 2001; Taylor & Grant 2004; Sim *et al.* 2005).

Recent studies have attempted to pinpoint the cause of the decline in Northern Lapwing numbers. Analysis ring recovery data from the past 30 years in Britain revealed that adult survival has increased from a life expectancy of 2.4 years to 3.5 years, and first year survival, although it has fluctuated from year to year, has not changed since 1930 (Peach *et al.* 1994; Catchpole *et al.* 1999). These results imply that Northern Lapwings are failing to produce enough young to maintain stable populations, and that poor breeding success up to, or just after time of fledging, is the most likely cause of decline.

Causes of Nest Failure and Chick Mortality

Because they are ground-nesting birds, Northern Lapwings are susceptible to nest loss for a wide variety of reasons, and their nest failure rates are relatively high. Although the causes of nest failure vary from study to study (often depending on the habitat in which the study was conducted) predation, nest destruction by farming activities and trampling by livestock are the most common causes (Galbraith 1988a; Baines 1990; Shrubb 1990; Berg *et al.* 1992; Fuller *et al.* 2002; Hart *et al.* 2002). Many studies point to the changes in agricultural practices as the reason for decreased nest survival. Increased agricultural intensification, including the switch from spring-sown crops in favour of autumn-sown crops, which has led to more uniform, denser and earlier, faster-growing crops, has reduced the amount of suitable nesting habitat, and the

length of time throughout the breeding season that suitable habitat is available (Shrubb 1990). Northern Lapwings show a strong preference for spring tillage, and avoid autumn tillage (Wilson *et al.* 2001). Tall swards may increase the likelihood of predators locating nests, chicks or adults by reducing adults' ability to spot approaching predators and uniform swards may increase the likelihood of predation by reducing cover and camouflage (Vickery *et al.* 2001). An experiment by Baines (1990) using Black-headed Gull *Larus ridibundus* eggs to simulate Northern Lapwing clutches revealed a higher predation rate of clutches on improved grassland compared to clutches on unimproved grassland. Changes in the timing of cultivation have led to an increase in the numbers of nests destroyed by farm machinery. Changes in the stocking densities of livestock (enabled by improving grassland through the application of nitrogen fertilisers) also had a negative effect on nest survival. Livestock may destroy nests directly by trampling and the manure produced by the livestock can cause an increase in soil invertebrates. This can lead to an influx of generalist predators such as Carrion Crows *Corvus corone*, increasing the predation pressure on the Northern Lapwing eggs and chicks (Vickery *et al.* 2001). The presence of livestock may also increase nest disturbance by forcing incubating adults to leave their nest more frequently, and the movement to and from the nests may attract the attention of predators (Hart *et al.* 2002).

Chick survival is the other important factor that influences Northern Lapwing productivity. Factors that influence chick survival include the weather, food availability and predation. Hudson *et al.* (1994) suggested that in many Northern Lapwing populations, chick survival might chiefly determine productivity. The ability of Northern Lapwings to lay replacement clutches may weaken the impact of nest losses to predators and farming activities, however, Galbraith (1988c) found that chicks which hatched from clutches laid later on in the breeding season had lower survival rates than chicks from early clutches. Egg volume has been shown to have a positive influence on chick survival up to ten days after hatching (Galbraith 1988a). Wader chicks rely on internal nutrient reserves for food during the first couple of days of life whilst they learn to catch prey items. Therefore, chicks from larger eggs will be larger in size at hatching, and will carry greater nutrient reserves such as proteins and lipids (Blomqvist *et al.* 1997), and have a better chance of survival, especially if broods have to move large distances between nest sites and suitable feeding grounds.

The survival of chicks that hatch on arable land is influenced by the proximity of pasture where higher densities of invertebrate prey are found (Galbraith 1988a), and poor chick survival from broods that hatch from later clutches may be due to a seasonal depletion in food availability (Galbraith 1988b).

Weather may also influence chick survival. During the first few days of life a chick's ability for thermo-regulation is poor, and they rely on brooding from parents for warmth (Beintema & Visser 1989). If broods have to move large distances to reach suitable feeding habitat then wet, cold weather, combined with the increased energy expenditure of chicks relying on yolk sacs, can result in high chick mortality. Wet weather also increases the need for brooding, which reduces the time chicks can spend foraging, leading to a possible reduction in chick growth and increased mortality. Alternatively, during periods of dry weather (when chicks are able to forage for longer periods between brooding) surface-living invertebrates become scarce and earthworms tend to bury further into the ground, making them unavailable to both chicks and adults.

Predation is another major cause of chick mortality. Many species prey on chicks (Trolliet 2003), although identifying Northern Lapwing chick predators is not an easy task (see Chapter 5) corvids, gulls *Larus*, foxes *Vulpes vulpes* and mustelids are believed to be important predators of Northern Lapwing chicks (Trolliet 2003), although this varies from region to region. Galbraith (1989a) noted that Carrion Crows, stoats *Mustela erminea* and foxes were the main predators in Scotland, whereas Berg *et al.* (1992) considered corvids the main predators in Sweden with predation by foxes being less important, probably due to a low fox population as a result of mange.

Population Dynamics

Various factors can influence the abundance and range of bird populations including food-supply, predation, parasitism, disease, weather and increasingly human impacts (extrinsic factors) resulting in changes in birth rates, death rates and movements (intrinsic demographic factors, Newton 1998).

The expectation of life for an adult Northern Lapwing increased from an average of 2.4 years (1909-52) to 3.5 years (1961-89). First year survival rates, although fluctuating year-to-year, appear relatively unchanged since 1930 (Peach *et al.* 1994). Thus, Northern Lapwing survival rates have improved during the main period of population decline in Britain.

Northern Lapwings are highly philopatric. Thompson *et al.* (1994) carried out a study on Northern Lapwings at two sites in the north of England. One site had a declining population, whereas the population at the second site was stable. They found that 95% of adults bred in natal or adjacent fields in consecutive years, illustrating a high degree of site faithfulness. Also, the return rates of young Northern Lapwing were higher than for other shorebirds (Thompson *et al.* 1994). Even with a large percentage of the population returning to the same site to breed in following years, there was no evidence of inbreeding between parents and siblings, although there is a potential risk of inbreeding between siblings from different years. Thompson *et al.* (1994) concluded that the stability of Northern Lapwing populations is largely dependent on the number of birds produced locally (local breeding success), and although immigration alone would not maintain a population, it may be important in the short-term in bolstering a declining population.

Bird populations can be influenced by the distribution of suitable habitat within the landscape, as well as the amount and quality of habitat (Newton 1998). Metapopulations are groups of subpopulations which exist in fragmented habitat patches but are linked by dispersal (Hanski 1998, Newton 1998). Within metapopulations there can be regular local extinctions and recolonisations and some sub-populations may be seen as sources, whilst others may be seen as sinks. Populations can be regulated by density-dependent factors and density-independent factors. Both can influence rates of population growth, but only density-dependent factors can regulate population size (Ricklefs 2001).

As suitable breeding habitat for Northern Lapwings has been more scarce and fragmented due to agricultural practices, populations are becoming more isolated, and metapopulation theory may become increasingly important in regard to Northern

Lapwing populations and initiating suitable conservation methods. With suitable nest sites on the decline, the territorial behaviour of the Northern Lapwing is expected to cause density-dependent competition for nest space. Galbraith (1988d) found no direct evidence that density-dependence influenced hatching or fledging success (which could result in population limitation), but found adult Northern Lapwings conformed to the ideal despotic distribution where better sites occupied first and late arrivals restricted to poorer sites for breeding or no sites at all, where they become non-breeders. Thus density-dependent effects through the exclusion of birds by territorial behaviour may explain the persistence of Northern Lapwings breeding in sub-optimal habitats. As the availability of optimal breeding habitats has been drastically reduced by the changes in agriculture, the need to identify and protect source populations and to aid the recolonisation of previously uninhabited suitable areas has become even more important. If habitat becomes too fragmented and subpopulations are too far apart to facilitate recolonisation, the local extinctions could accentuate population declines and range contractions.

Results and Discussion

Over recent decades population declines in UK-breeding Northern Lapwings have been most severe in Wales. Between 1987 and 1998 numbers of breeding Northern Lapwings fell by 77% from an estimated 7448 pairs to 1689 pairs (Wilson *et al.* 2001). The major habitat in Wales is grassland, whereas in England over a third of habitat is arable, and Scotland is dominated by upland habitats (Fig.1). However, even though grassland is the dominant habitat in Wales, habitat preference indices indicate that Northern Lapwings have a strong preference for nesting on arable land (although arable land is relatively scarce in Wales), and appear to actively avoid grassland (Wilson *et al.* 2001). Northern Lapwing numbers are declining, and arable land appears to be an important habitat for breeding Northern Lapwings. As concluded in this thesis, it is important that potential factors that may be influencing Northern Lapwing productivity are better understood if attempts to slow or reverse the decline through conservation initiatives are to be successful.

England *Wales* *Scotland*

Figure 1. Cover of broad habitat types within England, Wales and Scotland in 2001 (http://science.ceh.ac.uk/data/lcm/lcmleaflet2000/leaflet6.pdf). White: Arable & horticultural land; Black: Grassland (improved and neutral); Light grey: Mountain, moor, heath, down; Dark grey: Other (coastal, developed, inland water, woodland).

In Chapter 2 the efficacy of one such conservation initiative, the Northern Lapwing Recovery Project initiated by the Royal Society for the Protection of Birds across Wales between 1999 and 2001 is investigated. In Chapters 4 and 5 the breeding success of Northern Lapwings in an arable-dominated landscape in North Wales is addressed. A novel method for monitoring predation of Northern Lapwing nests using new digital camera technology incorporating video motion detection software which was field-trialled as part of my field-based studies is presented in Chapter 3. Finally Chapter 6 examines the decline of the UK Northern Lapwing population and investigate regional variations in demographic parameters with the intention of explaining, to some degree, the variation in Northern Lapwing population declines within different regions of the UK.

The Department for Environment, Food and Rural Affairs (Defra) now uses wild bird population trends as a 'headline indicator' of the sustainability of its policies and 'quality of life' in the UK (Anon. 1999). The Northern Lapwing is one of eighteen species which form the Farmland Bird Index, which in turn is a subset of species classified as indicator species. The dramatic decline of many bird species associated with lowland farmland is an important conservation issue in Britain and elsewhere in Europe. In 2000, Defra adopted a Public Service Agreement (PSA) target which

involves reversing the long-term decline in the number of farmland birds in England by 2020 (Gregory *et al.* 2004).

Schemes now exist across Britain where farmers and land owners can enter into an agreement with the government wherein payments are made to farmers and other land managers to enhance and conserve landscapes, their wildlife and history. The agri-environment scheme which currently exists in Wales is Tir Gofal. Within the Tir Gofal scheme and other agri-environment schemes (the Environmental Stewardship scheme in England and the Rural Stewardship scheme in Scotland and Environmentally Sensitive Areas (ESAs)) farmers have the option of voluntarily signing up to conservation prescriptions aimed specifically at Northern Lapwings.

The Northern Lapwing Recovery Project (Chapter 2) implemented in Wales in 1999 and maintained for three years encouraged farmers and land managers to deliver suitable Northern Lapwing breeding habitats through various conservation initiatives, including agri-environment schemes. Generalised Linear Mixed Models were used to assess the effectiveness of habitat management in maintaining stable numbers or increasing numbers of breeding Northern Lapwings, and whether habitat management positively influenced Northern Lapwing productivity.

One criticism of agri-environment schemes is that the research designs are often inadequate to assess reliability of the effectiveness of such schemes and in many cases no attempts were made to monitor the effects of habitat management on the target species (Kleijn & Sutherland 2003). The one advantage of the Wales Recovery Project dataset was that many sites were monitored before going into Northern Lapwing-specific habitat management. Therefore, it was possible to compare the 'before and after' effects of management. It was not possible to detect any effect of management *per se* on either Northern Lapwing breeding numbers or Northern Lapwing productivity. However, the number of breeding Northern Lapwings on nature reserves did decline at a slower rate than Northern Lapwings breeding on non-reserve sites.

The lack of evidence indicating different productivity between nature reserves and non-nature reserves suggests that breeding numbers on reserves may be due to an

influx of adults from surrounding areas. Nature reserves can play an important role in maintaining sub populations, and therefore enabling dispersal and recolonisation of suitable habitat in the event of local extinctions. However, nature reserves on their own should not be relied upon to maintain populations of any species. In light of Northern Lapwing's preferences for breeding on arable land in Wales, the fact that conservation initiatives did little to reverse current population declines in the wider countryside is a cause for concern.

The ability of Northern Lapwings to produce sufficient young is vital, if populations are to remain stable. Peach *et al.* (1994) calculated that given estimated first year and adult survival rates, Northern Lapwings would need to successfully raise 0.83 chicks per pair annually to maintain populations at current levels. The fact that over two-thirds of all sites monitored as part of the Northern Lapwing Recovery Project in Wales failed to reach these required levels of productivity further highlight the need to critically assess key stages of breeding with an attempt to more fully understand what factors are driving low breeding success.

Northern Lapwing breeding success was monitored in two successive years at four sites in North Wales. These sites were located in a low-lying agricultural landscape around the Dee Estuary. During the Northern Lapwing Recovery Project, this area was identified as one of the few remaining key breeding areas for Northern Lapwings in Wales. Northern Lapwing breeding habitat preferences and nest survival rates (Chapter 4), and chick growth rates, body condition and mortality rates (Chapter 5) were assessed. It was found that Northern Lapwings exhibited a strong preference for breeding on spring cereal above winter cereals and grass which is in agreement with the findings by Wilson *et al.* (2001).

Northern Lapwing nests can fail to survive until hatching for various reasons. The main causes of nest failure were trampling by livestock (failure rates ranging between 0-22%: Trolliet 2003), destruction by farm machinery (failure rates between 0-49.9%: Trolliet 2003) and predation (9-49.7%: Trolliet 2003). The main cause of nest failure in the North Wales population was predation. The novel use of digital nest cameras employing video motion detection and infra-red triggering mechanisms allowed the identification of the main species preying upon Northern Lapwing eggs. Mammalian

species, especially foxes, were found to be the main predators. Higher nest predation rates near the time of hatching in comparison to the egg laying and incubation periods suggest that predators could be using acoustic rather than visual cues to locate nests, which also implies predation by mammalian rather than avian species. The use of a remote system to identify nest predators (Chapter 3) circumvents any potential bias in observer identification of predators, whereas the presence of cameras next to nests did not appear to influence nest predation rates.

Predation was also found to be the main cause of chick mortality (Chapter 5). The extent to which predators were responsible for chick losses was exceptional. Although predation was reported as the major cause of wader chick mortality in other studies (Miller & Knopf 1993; Grant *et al.* 1999; Kruse *et al.* 2001; Hart *et al.* 2002; Sheldon 2002), chick predation in the present study was so great that less than 1% of chicks survived until fledging.

My view is that controlling known predators may not improve chick survival. Firstly, the identification of species that prey upon Northern Lapwing chicks is still relatively unknown. There are more species known to prey upon chicks than are known to take eggs (Trolliet 2003). Secondly, little is known about the interaction between different predator species and Northern Lapwings. For example, it is feasible that if fox numbers were reduced, then numbers of mustelids (further predators of Northern Lapwing chicks), which would normally be depressed by the presence of a larger predator, could increase and the overall impact on chick survival would be minimal. Indeed, there is limited evidence from an eight-year predator control experiment carried out by the RSPB that this may be the case (M. Bolton, pers. comm.). Finally, assessing the causes of mortality in a bird population is not always straightforward (Newton 1998). Chicks were found generally to be in poor body condition and had slower growth rates relative to previous studies (Redfern 1983; Beintema & Visser 1989) suggesting that chicks were unable to find sufficient food to sustain healthy growth. These results suggest that although predation is the proximate cause of chick mortality, starvation through the lack of available food, potentially mediated by land-use changes, may be the ultimate cause of death.

Recent work by Chamberlain & Crick (2003) using the British Trust for Ornithology's nest record scheme indicates that nest predation rates throughout the UK increased in the 1990's, and these elevated predation rates may be partially responsible for recent population declines. The major results from studying Northern Lapwing breeding success suggest that predation is a major factor influencing the survival and hatching success of Northern Lapwing nests and particularly chick survival rates. Overall, nest survival rates were generally quite low, and chick fledging success was extremely low. This suggests that although nesting success may play some role in determining Northern Lapwing breeding success, predation pressure on chicks appears to be the major factor determining productivity within a declining Northern Lapwing population in Wales.

Although Northern Lapwing populations in Wales have undergone the greatest decline in breeding numbers, populations throughout the UK have also declined, although to a varying extent. Whether variation in demographic parameters could explain the different rates of population decline among regions was assessed. For any population, whether birds or other animals, to remain stable the inputs (from births and immigration) must equal the losses (from deaths and emigration). Using Nest Record Card Scheme and Ring Recovery datasets of the British Trust for Ornithology (Chapter 6), productivity levels (as a measurement of nesting success), movement of birds among regions and death rates (first-year and/or adult survival rates) were examined to assess whether they differed among regions.

Nest success did not explain regional population declines. The assessment of productivity was not complete. Northern Lapwing chicks are precocial and a newly hatched brood often leave the nest scrape within hours of hatching. Consequently, collecting reliable data on chick survival from hatching to fledging is difficult. The only data that exist on chick survival result from relatively small, localised studies and there is no UK-wide dataset. Recruitment in the Northern Lapwing is mainly driven by philopatry yet populations with poor local breeding success may be maintained in the short-term by some degree of immigration (Thompson *et al.* 1994). However, no evidence was found of birds moving to breed in areas with low productivity (a sink population). This may be a reflection of the fact that all regional populations are

declining, therefore productivity (highlighted as the main driving force behind recent population declines – Peach *et al.* 1994), and recruitment is low in all regions.

Interestingly, nesting success, as calculated from the Nest Record Card Scheme, was relatively high across all regions in comparison to estimates from previous studies (Trolliet 2003). This can be interpreted in two ways: 1) productivity is largely determined by chick survival rather than nest survival, or 2) estimates of nesting success derived by previous studies are taken from declining populations and therefore these estimates are not reflective of nesting success in healthy, stable populations. Evidence suggests that chick mortality is the main determinant of poor productivity (Chapter 5; Trolliet 2003), but also that the majority of studies on Northern Lapwings are carried out in western European countries where populations, like the UK populations, have undergone recent widespread declines.

The role of agricultural intensification in the decline of farmland bird populations has been widely reported (Fuller *et al.* 1995; Donald *et al.* 2000; Donald *et al.* 2002). The finding that nesting habitat influences nesting success and that the proportion of Northern Lapwings breeding in unsuitable grassland habitats has risen over recent years, possibly due to the loss of more suitable spring tillage (Chapter 6) highlights the fact that intensive farming has still an important influence on Northern Lapwing breeding success.

Concluding Remarks

The broad aims of this thesis were 1) to assess different aspects of Northern Lapwing breeding ecology in the attempt to add to our understanding of their demography and the underlying causes of the species' recent decline, and 2) to quantify the effects of a conservation initiative set up with the aim of slowing or reversing population declines in the hardest hit region Wales. As Northern Lapwings are a headline indicator species, it is of interest not only to conservation bodies, but also the government, that attempts are made to slow and hopefully reverse their continuing decline.

From this research it is apparent that the current levels of productivity within the Northern Lapwing population in North Wales are insufficient to maintain a stable

breeding population. Evidence from estimates of regional population declines and demographic parameters suggest that the same may be true for other Northern Lapwing populations throughout the United Kingdom. Nest survival rates are comparable to those reported in previous studies, although it is not always clear whether the studied populations where stable or in decline. Chick survival rates are much lower than those reported in previous studies and chick mortality is the main determinant of Northern Lapwing productivity in North Wales. The importance of chick survival, rather than nest survival, in determining annual productivity is further highlighted in Chapters 2 & 6.

Predation is a major determinant of both nesting success and survival of Northern Lapwing chicks in an agricultural landscape. Mammalian predators (e.g. foxes and badgers) in particular have a large influence on nest survival. Although it is not clear to what extent mammalian predators are responsible for high chick mortality rates, mammalian predators are, to some extent, responsible for Northern Lapwing chick mortalities. Predation has always been regarded as an important factor in determining the breeding success of not only Northern Lapwings but other bird species including Grey Partridges *Perdix perdix* (Tapper *et al.* 1996), Blackbirds and Song Thrushes *Turdus philomelos* (Paradis *et al.* 2000), Red Grouse *Lagopus lagopus* (Thirgood *et al.* 2000), Golden Plover *Pluvialis apricaria* (Parr 1992) and Eurasian Curlew (Grant *et al.* 1999). This study shows how predation (particularly of chicks) is the main proximate cause of Northern Lapwing breeding failure, although land-use changes resulting in low food availability and ultimately starvation may be the ultimate cause of poor breeding success. However, nest success will still impact upon productivity to a certain extent, and the use of remote devices such as the digital nest camera trialled as part of this research (Chapter 3) have been shown to be beneficial.

Variations in demographic parameters could not explain the variation among the rates of regional population declines. Northern Lapwing populations across all regions within the United Kingdom have undergone declines in breeding numbers over recent decades with poor productivity as the main intrinsic factor driving these population declines. It is probable then that all populations at the regional level can be regarded 'sink' populations resulting from continued low productivity. There is also a

suggestion that chick mortality rather than nest failure rates may be the main determinant of Northern Lapwing productivity at the regional level.

The ultimate aim of this PhD research is to provide valuable information on the causes of poor breeding success, and the extent to which low productivity is responsible for recent population declines with the aim of using these data to construct and implement effective conservation measures. A previous attempt to slow or reverse the decline in breeding numbers in Wales was not successful. In the absence of any assessment of habitat condition it was not clear whether the failure to reverse Northern Lapwing declines resulted from inadequacies in creating suitable habitat (i.e. in translating management advice into habitat improvement), or rather, whether suitable habitat was indeed created, but other over-riding factors (such as effects of climate and/or predation) resulted in continued low productivity. On the whole, conservation measures and agri-environment schemes aimed at a wide range of other species appear to have had a positive impact on the target species, although some schemes had a detrimental effect (see Kleijn & Sutherland 2003). However, a lack of sufficiently rigorous studies limits the assessment of the efficacy of such schemes (Kleijn & Sutherland 2003). Although the Northern Lapwing Recovery Project failed to reach its target, it highlighted the importance of 1) basing conservation measures on sound scientific research, and 2) properly monitoring such schemes in order to assess their effectiveness.

Any future conservation initiatives must take into account the impact of predators on Northern Lapwing populations, and also how the lack of food resources may increase predation rates. Although this research provides an insight into the role of breeding success in Northern Lapwing population declines, and the environmental factors that can influence breeding success, it raises further questions.

Firstly, one of four study sites where fieldwork was carried out was in an agri-environment scheme, yet breeding success across all sites was extremely low. This implies that the agri-environment scheme measures were ineffective. Therefore, further research into the benefits of Northern Lapwing and other farmland bird measures incorporated into such schemes is vital if these schemes are to work.

Secondly, the impact of different predator species on nest survival and chick survival remains to be explained. Although the identification of nest predators were elucidated through the use of digital nest cameras, this is only one study carried out in a single year. The identification of chick predators remains unknown, and given the importance of predation in determining chick survival, an attempt should be made to evaluate this issue.

Thirdly, a study on food availability for Northern Lapwing chicks in relation to agricultural practice, crop type and the abundance of different predator species should be carried out with the aim of investigating chick vulnerability to predation under varying environmental conditions.

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Chapter 2.

Failure of conservation management to improve Northern Lapwing *Vanellus vanellus* breeding success or population trends in Wales

Fiona Sharpe, Mark Bolton, Tamás Székely & Tony Pickup

Abstract

In response to recent Northern Lapwing population declines, the Royal Society for the Protection of Birds has initiated a number of regional and country "Recovery Projects" which aim to deliver suitable land management on a wide scale, by providing advice to farmers and facilitating entry into agri-environment schemes as appropriate. In Wales, Northern Lapwing declines have been particularly severe: a 77% reduction in breeding numbers between 1987 and 1998. A Recovery Project for Northern Lapwings in Wales operated from 1999 to 2001 and data were collected on counts of breeding Northern Lapwings and chicks, predators, livestock, land use and management prescriptions between 1998 to 2003. We use Generalized Linear Mixed Models to assess whether Northern Lapwing productivity and population trends were higher on sites where management had been carried out. During the course of the Recovery Project, Northern Lapwing breeding numbers on managed sites declined at a similar rate as those on unmanaged sites, however, declines on nature reserves were slower than declines on non-reserve sites. Whilst breeding densities and breeding success tended to be slightly higher at more southerly latitudes, population declines were more extensive at southerly locations than in northern Wales. Two-thirds of all sites failed to rear sufficient young each year to replace annual mortality, and there was no significant impact of conservation management on Northern Lapwing productivity. In the absence of independent assessment of habitat condition for breeding Northern Lapwings on managed and unmanaged sites, it is not clear whether the failure of conservation management is due to inadequate implementation of management recommendations, or whether other factors, such as climate change or excessive losses to predation, are annulling the effect of any habitat improvement.

Introduction

Many species of birds associated with farmland have undergone widespread declines in abundance and range size in Britain and Europe over the last three decades (O'Brien & Smith 1992; Fuller *et al.* 1995; Chamberlain *et al.* 2000; Wilson *et al.* 2001; BirdLife International 2004). There is a growing awareness that these declines are linked with modern agricultural practice (Chamberlain & Fuller 2000; Chamberlain *et al.* 2000; Donald *et al.* 2001; Robinson & Sutherland 2002; Benton *et al.* 2003). The changes in farmland management that have been implicated in farmland bird declines include: the agricultural improvement of pasture; increases in livestock densities; advancement in the timing of sowing and harvesting operations; the regional polarisation of arable and pastoral systems; the simplification of crop rotations and increases in fertiliser application (Baines 1990; Chamberlain *et al.* 2001; Stephens *et al.* 2003). The mechanisms by which these changes in management have affected bird populations vary between species (Chamberlain *et al.* 2001), and can operate at different stages of the life cycle (Siriwardena *et al.* 1999a, 1999b). Whilst many studies have focused on declines in farmland passerines (Evans 1997; Chamberlain & Siriwardena 2000), a number of wader species have also been affected by changes in farmland management (Wilson *et al.* 2005).

Over the past few decades, the numbers of breeding Northern Lapwings (*Vanellus vanellus*) in the UK have declined dramatically (Crick *et al.* 2004). Between 1987 and 1998 there was a 49% decline in Northern Lapwings across England and Wales, with the most severe decline occurring in Wales, where numbers fell by 77% (Wilson *et al.* 2001). Poor breeding success up to, or just after the time of fledging, has been the most likely contributory factor in this (Baines 1990; Peach *et al.* 1994; Catchpole *et al.* 1999), and the decline would have been more marked if not for the fact that adult survival rate has improved over the past 30 years from a life expectancy of 2.4 years to 3.5 years (Peach *et al.* 1994; Catchpole *et al.* 1999).

Potential causes of poor breeding success

Nest losses from farm work in nesting fields, desertion, trampling by livestock and predation are the principle causes of low nest survival (Baines 1990; Shrubb 1990; Berg *et al.* 1992; Trolliet 2003; Chamberlain & Crick 2003). Whilst the causes of

clutch failure are relatively simple to determine, the causes of chick mortality are more difficult to investigate.

Northern Lapwing Recovery Projects

Increasing concern over the impact of agricultural intensification on farmland bird species has led the Royal Society for the Protection of Birds (RSPB) to establish initiatives aimed at improving breeding success of Northern Lapwings on farmland. Such country and regional 'Northern Lapwing Recovery Projects' involve working with farmers and land managers to maintain or create suitable nesting and chick-rearing habitats for Northern Lapwings, through a mixture of direct advice to farmers, facilitation of entry into agri-environment schemes, and the funding of small-scale management projects. In Wales, where the Northern Lapwing population dropped from an estimated 7448 pairs in 1987, to 1689 pairs in 1998, a Recovery Project operated between 1999 and 2001. The scheme aimed to identify key sites (those holding more than 10 breeding pairs), and to implement appropriate management to create or enhance habitat conditions necessary for successful breeding.

This study examines the impact of Northern Lapwing management on breeding productivity and population size from data collected over six years encompassing the operation of the Recovery Project in Wales, both from sites where Northern Lapwing management was carried out, and those where no conservation actions were implemented. We also examined the relationships between predator densities, habitat and land-use and Northern Lapwing breeding productivity and density.

Methods

The Northern Lapwing Recovery Project in Wales identified 237 breeding sites, which represented an estimated 80% of the total number of Welsh breeding localities. Of these, 49 sites had data on breeding Northern Lapwings available for three or more years during the period 1998 to 2003. These sites ranged from whole farms to single fields and in 1999, they jointly held an estimated 33.5% of breeding Northern Lapwings in Wales (relative to the 1998 survey sample estimate, Wilson *et al.* 2001). These sites were geographically representative of all Northern Lapwing sites in Wales and included a range of land uses, ownership and Northern Lapwing management.

Study Design

Studies of the evaluation of the impact of conservation management, particularly in relation to the implementation of agri-environment schemes, have frequently been criticised for lack of adequate replication of treatments, the absence of unbiased "controls" and lack of robust, statistical analysis (Kleijn *et al.* 2001; Kleijn & Sutherland 2003). The study design adopted here compared breeding density, population trend and productivity of Northern Lapwings on 28 sites that underwent some form of management for Northern Lapwings during the period 1998 to 2003 with the 21 "control" sites for which data were available, that had similar geographic spread and habitat types, but were not subject to special conservation management during this period. See appendix (pages i-ix) for site details.

Habitat management

Of the 28 sites that underwent management, 12 were classified as "part-managed" since management actions were undertaken to create suitable nesting (but not chick rearing) habitat at some point during the period 1999 - 2003. Such management included rush-cutting, over winter-grazing regimes to create a short sward for the breeding season, removal of potential avian predator perches, a return to spring-sown crops, and livestock exclusion during the breeding season. The remaining 16 "fully-managed" sites underwent management to create habitat suitable for both nesting and chick rearing. Such management included the prescriptions carried out on part-managed sites, plus creating wet areas through reduced drainage and creating shallow scrapes, profiling ditch banks, and also leaving areas as set-aside. No sites underwent management to provide chick habitat only. The year in which sites entered into Northern Lapwing management varied, and not all sites were actively managed during every year of the Recovery Project (1999 – 2001), or subsequently. For managed sites, site-years were therefore coded to reflect whether management had yet to be initiated; was ongoing; or ceased for each year from 1998 to 2003.

Data collection

Visits to breeding sites were made by volunteers and RSPB staff throughout the period of the Recovery Project (1999-2001), and 46 sites out of 49 sites continued to be monitored after this period (2002-2003). Records of breeding Northern Lapwings also exist for most sites prior to the start of start of the Recovery Project. Sites were

visited up to five times throughout the breeding season, with each survey being carried out between specified dates between mid March and early July. Data were recorded on the number of adult Northern Lapwings; the number of adult Northern Lapwings with chicks; the number and age of chicks (newly-hatched, well-grown, fledged); the number of Carrions Crows (*Corvus corone corone*); the number and species of other predators; the number (or presence) of sheep and livestock. The number of breeding pairs of Northern Lapwing was calculated following O'Brien & Smith (1992). Breeding success was assessed from the number of adult Northern Lapwings with broods late in the breeding season. Since the behaviour of breeding Northern Lapwings changes markedly when they have hatched young (Cramp & Simmons 1983) the number of adults accompanied by broods can be readily determined and this method provides a reliable index of breeding success (see Grant *et al.* 2000). The number of adult Northern Lapwings with young was expressed relative to the size of the breeding population to provide an index of breeding success per female. Conservation management actions and habitat types were recorded for all sites. A wide variety of habitats were recorded, so for analytical purposes, habitats were classified as either improved grassland, arable, extensive grassland (including rough pasture, heath, industrial waste ground), a mixture of improved grass and arable, a mixture of improved and extensive grassland, and a mixture of arable and extensive grassland.

Data Analysis

Generalised Linear Mixed Models (GLMMs) that specified site as a random effect were used to investigate the relationship among explanatory variables and breeding densities of Northern Lapwings and their productivity. In analyses of Northern Lapwing population density, the model employed a Poisson error structure, a log link and the natural log of the site area as an offset. For analysis of productivity in which the response variable was the number of chicks reared to fledging on the site, a Poisson error structure was employed, with the natural log of the number of breeding pairs as an offset. Explanatory variables included in the maximal model were: management designation (whether a site was unmanaged throughout the study period, prior to management, undergoing part-management, undergoing full-management or post-management); presence of sheep and cattle; latitude; counts of potential predators; habitat; the presence of wet features and site designation (whether the site

was managed as a nature reserve). Year was specified as a class variable for analyses of productivity, and as a covariate for analysis of population trend (see below). All explanatory variables plus interactions of interest, were included in the initial maximal model, and then the variable with the highest non-significant *P*-value was excluded from the model and the model was re-run. This process continued until all explanatory variables left in the model were significant at $P < 0.05$. GLMMs were run using the GLIMMIX macro procedure in SAS version 8.2 (Littell *et al.* 1996).

Results

Management for Northern Lapwing

Almost half of the 28 sites that were targeted for Northern Lapwing management during the period of the Recovery Project (1999 – 2001) were managed by conservation organisations or farmers sympathetic to conservation, and were therefore subject to management for breeding waders in 1998, prior to the onset of the project (Fig. 1). As management for Northern Lapwings was progressively instigated on other sites during the course of the Recovery Project, the percentage of sites that were managed annually for Northern Lapwings rose to 89%. The remaining 11% refer to sites managed in the earlier years, where management ceased.

We found weak evidence that management tended to be directed at sites that already held the highest densities of Northern Lapwings. Among the 29 sites surveyed in 1998 that were not undergoing any management for Northern Lapwing at that time, those where management subsequently took place had a tendency to hold higher densities of breeding Northern Lapwings in 1998 than those where no management subsequently occurred (0.59 ± 0.16 (SE) and 0.26 ± 0.05 (SE) pairs/ha respectively, t-test for unequal variance $t_{5.75} = 2.01$ $P = 0.062$).

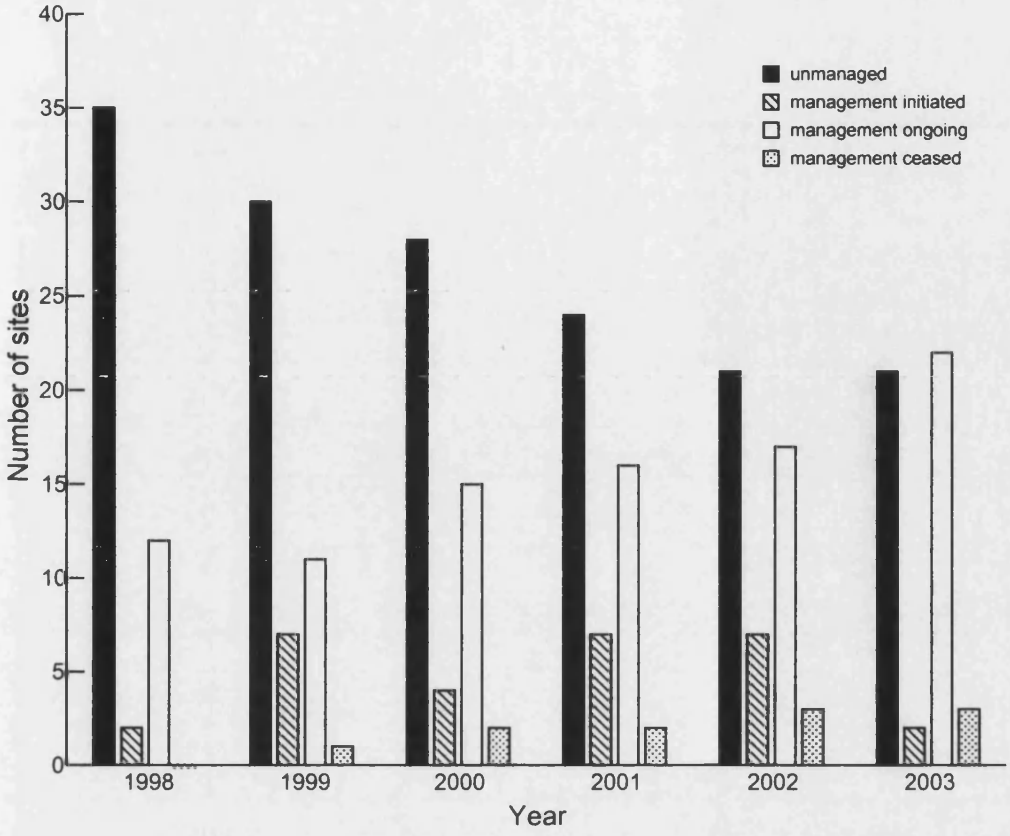


Figure 1. The number of sites in four management categories (unmanaged, management initiated, currently managed, management ceased) in Wales between 1998 and 2003.

Did Recovery Project reverse Northern Lapwing declines?

Breeding densities of Northern Lapwings on managed sites declined at a similar rate to those on unmanaged sites between 1998 and 2003 (Fig 2). GLMM analysis indicated that Northern Lapwing breeding density declined significantly with year ($F_{1,178} = 5.49$, $P = 0.0202$), but was not related to the implementation of active, current management for Northern Lapwings ($F_{4,169} = 1.45$, $P = 0.2193$). Those sites that were managed throughout as reserves did not support higher densities of breeding Northern Lapwings (Fig. 3, $F_{1,79.1} = 2.47$, $P = 0.1203$), although, during the study period Northern Lapwings declined at a slower rate on reserves than on non-designated sites (Fig. 4, year * designation interaction $F_{1,178} = 5.87$, $P = 0.0164$). There was a statistically significant effect of latitude on Northern Lapwing population size with more southerly sites holding higher densities of breeding Northern Lapwings than

more northerly sites ($F_{1,74.7}$ = 4.81, P = 0.0314). However, Northern Lapwings breeding density declined at a faster rates on more southerly sites compared to more northerly sites (Fig. 4, year * latitude interaction $F_{1,178}$ = 5.39, P = 0.0213). Northern Lapwing population density was not related to any other explanatory variables considered. See appendix (page x) for details of full and final models.

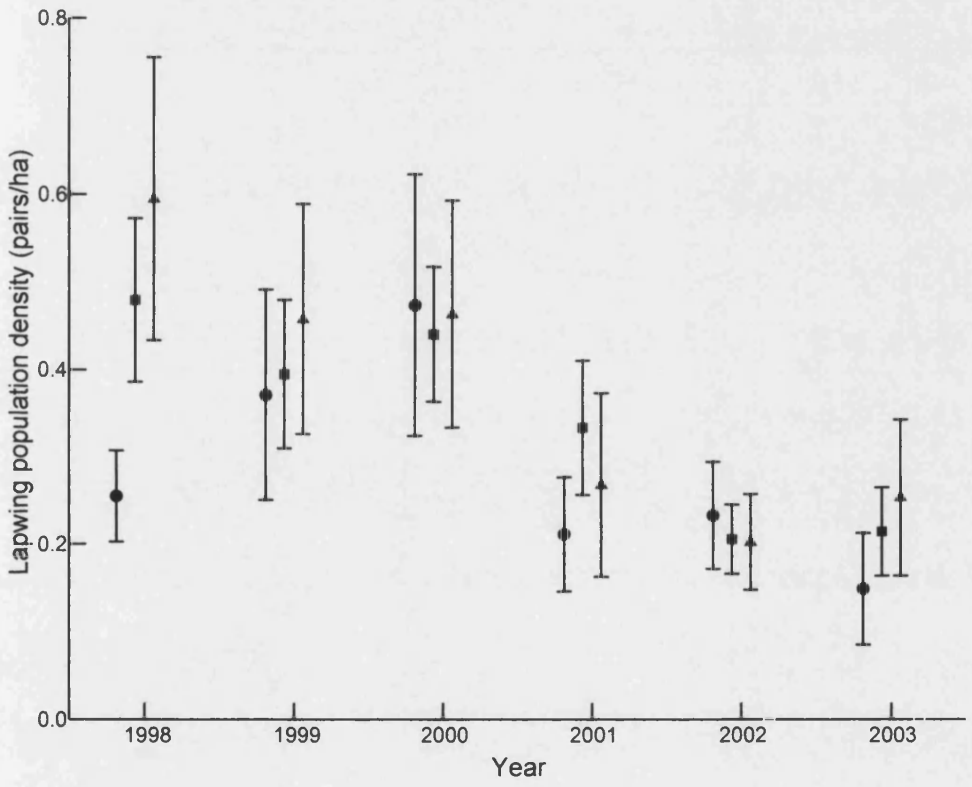


Figure 2. Northern Lapwing population density (mean ± 1 SE) on unmanaged and managed sites. ● = unmanaged sites, ■ = all managed sites, ▲ = sites managed after 1998 only.

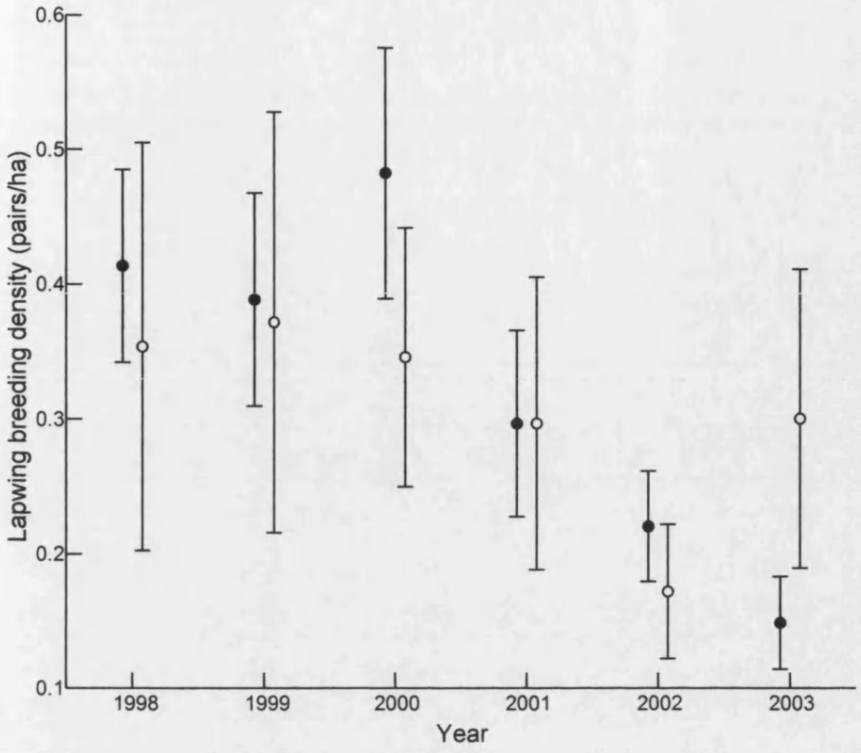
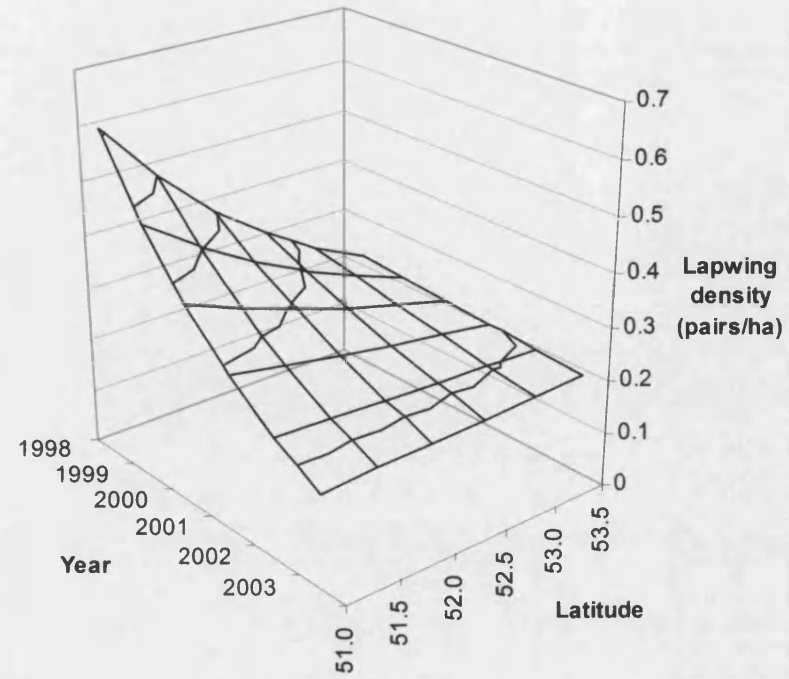


Figure 3. Northern Lapwing population density (mean ± 1 SE pairs/ha) according to site designation. ● = non-reserve sites, ○ = nature reserves.

Pooling all available data from both managed and non-managed sites indicated that the annual rate of decline between 1999 and 2003 was 12%, which is similar to the rate associated with the population reduction occurring between 1987 and 1998, i.e. 13% per annum. Thus, there is no evidence that recovery measures have improved the conservation status of Northern Lapwings over all monitored sites in Wales, or even within the group of sites where management was implemented between 1998 and 2003. We further considered whether the introduction of management to the 14 sites that had previously not been managed for Northern Lapwings produced any benefit: however Northern Lapwing populations on these sites showed similar declines to those on unmanaged sites (Fig. 2).

a)



b)

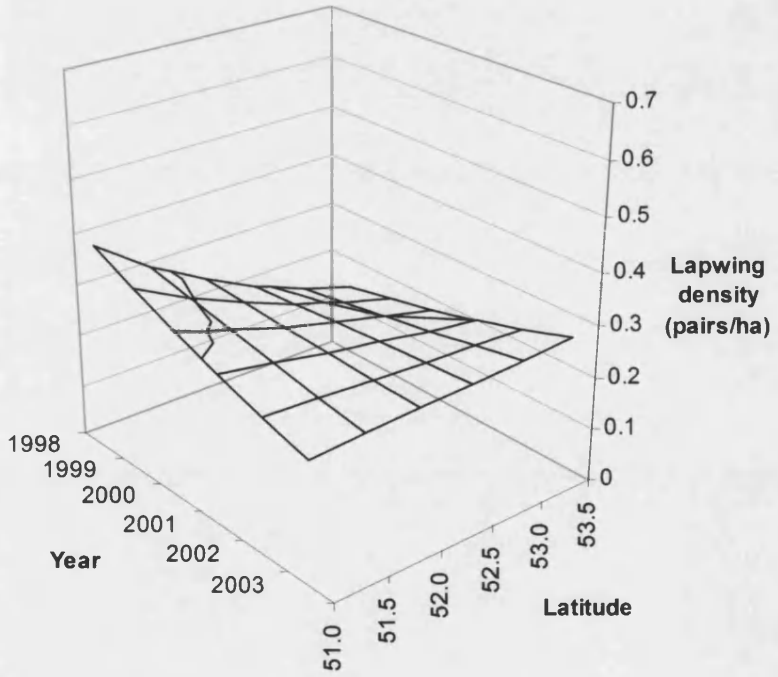


Figure 4. Northern Lapwing population density trends (model predicted values) in relation to latitude (°) between 1998 and 2003 according to site designation. (a) non reserves; (b) nature reserves.

Effect of management on Northern Lapwing productivity

There were significant differences in levels of productivity among years ($F_{5,124} = 5.44$, $P = 0.0001$): more young were reared per pair in 1999 than in 2000, 2002 and 2003. However, even in this year of relatively high productivity, the number of young fledged (mean of 0.54 chicks per pair) was still below the level required to maintain a stable population (0.83 chicks per pair: Peach *et al.* 1994). The rates of population decline described above are consistent with a complete absence of recruitment of young birds into the breeding population. GLMMs indicated that in addition to differences among years, there was a statistically significant effect of breeding latitude on productivity (Fig. 5): the most southerly sites averaged 0.52 young fledged per pair across all six years, whereas the most northerly fledged only 0.24 young per pair ($F_{1,38.4} = 9.12$, $P = 0.0045$). There were no differences in productivity in relation to the occurrence or type of conservation management ($F_{4,86.3} = 1.41$, $P = 0.2358$). See appendix (pages x-xi) for details of full and final model.

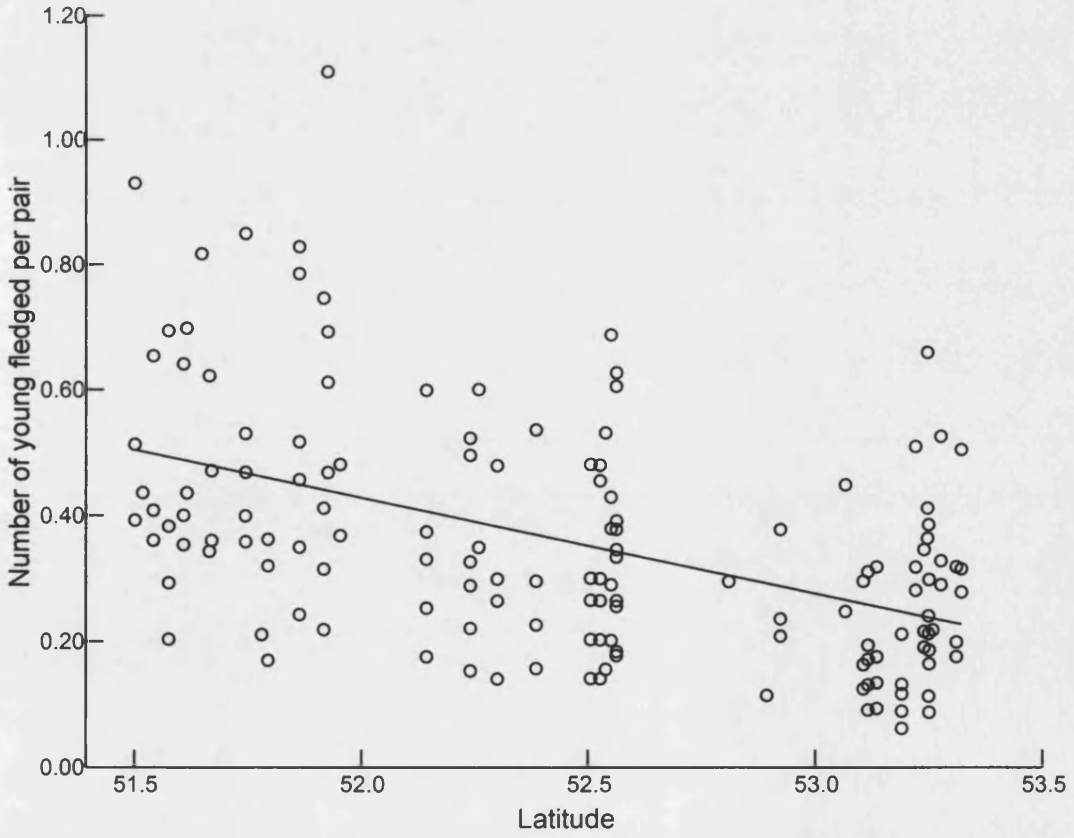


Figure 5. The relationship between Northern Lapwing productivity (the number of young fledged per pair) and latitude (°).

Discussion

There was no evidence that conservation management increased Northern Lapwing productivity or reversed population declines on 28 sites in Wales. Whilst populations of Northern Lapwings breeding on nature reserves declined at a slightly slower rate than populations breeding on commercially farmed land, there was no evidence to suggest that nature reserves held higher breeding densities of Northern Lapwings, or that they had a positive influence on population trends. Whilst there was evidence that populations further south fledged more young per pair than those further north, levels of productivity were generally low, well below the level required to maintain a stable population. Although more southerly sites fledged more young per pair, and generally held higher breeding densities of Northern Lapwings, population trends suggested that Northern Lapwings breeding further south in Wales declined at a faster rate than Northern Lapwings breeding further north. Rates of population decline from 1998 to 2003 were similar to those occurring between 1987 and 1998 (Wilson *et al.* 2001), and consistent with a virtual absence of recruitment of young birds into the breeding population (Catchpole *et al.* 1999). Population declines of Northern Lapwings in Wales may therefore be explained by extremely poor breeding success, and the lack of any clear relationship between productivity and habitat type suggests that the drivers of low productivity are likely to be generic, rather than associated with any one specific type of land management or agricultural practice. However, the fact that populations breeding further south fledged more young per pair yet declined at a faster rate suggests that that factors other than just poor breeding success play a role in influencing the rate of Northern Lapwing population decline.

Around 96% of the Northern Lapwing breeding population of England and Wales nest on agricultural land (Shrubb & Lack 1991). The widespread distribution of breeding sites and the species' preponderance to change location between years in response to local habitat conditions (Thompson *et al.* 1994; Berg *et al.* 2002) requires that any measures to reverse population declines be implemented on an appropriate scale, both spatially and temporally. Whilst nature reserves may have an important role in maintaining the geographic range of the species, in areas where populations on commercial farmland are unviable, reserves alone will clearly be inadequate to maintain national populations. The use of agri-environment prescriptions to deliver

suitable habitat therefore represents the only feasible mechanism for wide-scale reversal of Northern Lapwing populations.

It is of considerable concern that the current study has failed to demonstrate any positive impact of Northern Lapwing management, delivered primarily through agri-environment mechanisms, on a total of 28 sites in Wales. These results are in broad agreement with a number of similar studies carried out in the UK and the Netherlands. Ausden & Hirons (2002) have shown that the Environmentally Sensitive Area (ESA) agri-environment scheme has failed to reverse Northern Lapwing declines on lowland wet grassland, outside of RSPB reserves, in four areas of England (Broads, Somerset Levels and Moors, Suffolk River Valleys and Upper Thames Tributaries). Examination of Northern Lapwing population trends between 1994 to 1996 within the North Peaks ESA in the UK, revealed that ESAs had lower densities of breeding Northern Lapwings than control sites (ADAS 1997, cited in Kleijn & Sutherland 2003). The Breeding Waders of Wet Meadows surveys also revealed declines in four of five ESAs between 1982 and 2002 (Wilson *et al.* 2005). Kleijn *et al.* (2001) and Kleijn & Van Zuijlen (2004) have similarly found agri-environment schemes were ineffective in protecting meadow birds in The Netherlands. By contrast, in England, Bradbury & Allen (2003) found significantly higher densities of Northern Lapwings on farms in agri-environment management than on controls, but did not compare productivity.

Gates & Donald (2000) examined geographic variation in Northern Lapwing declines in Wales and England between the period of the two UK Breeding Bird Atlases (1968–72 and 1988-91) and on the basis of the correlates of the extent of decline during this period, predicted future extinction probabilities for each 10km tetrad in the UK that still held breeding Northern Lapwings in the latter period. Using a Principal Component Analysis, they found that high extinction probabilities for Northern Lapwings were associated with higher temperatures, lower rainfall, lower altitude, large areas devoted to cereals or non-cereal crops, and little area devoted to rough grazing or fallow. Extinction probabilities were highest in the south and west of UK and most occupied tetrads within Wales were classified with the highest extinction probability.

In the absence of any assessment of habitat condition on commercial farmland or nature reserves in the present study, it is not clear whether the failure to reverse Northern Lapwing declines results from inadequacies in creating suitable habitat (i.e. in translating management advice into habitat improvement), or rather, whether suitable habitat was indeed created, but other over-riding factors (such as effects of climate and/or predation) resulted in continued low productivity. It is notable in this context, that nature reserves did not support higher densities of breeding Northern Lapwings than commercial farmland and population continued to decline on nature reserves, although at a slower rate, suggesting that factors other than the creation of suitable habitat were responsible for continuing population declines. Latitudinal variations in productivity and population trends are more difficult to explain. Climate change is likely to induce changes in the phenology of invertebrate prey for Northern Lapwings, as has been documented for Golden Plover (*Pluvialis apricaria*) (Pearce-Higgins *et al.* 2005). Such changes are likely to have a detrimental effect on the suitability of breeding habitat, although the population effects and regional variation in their impact have yet to be examined in detail. It is at least plausible that the population declines occurring in Wales have been exacerbated by climate change. The existence of any variation in adult and juvenile over-winter survival and natal philopatry could also explain some of the latitudinal variation in population trends. If there is a tendency for birds breeding in the south to move to more northerly locations, or a tendency for birds to migrate to breeding sites in North Wales from other parts of the UK then this could in some way compensate for lower breeding success of northerly populations. Alternatively, population declines driven by poor breeding success could be exacerbated in the south by lower adult or first year over-winter survival rates. Around of third of Northern Lapwings breeding in Britain over-winter in Britain. The remaining birds tend to move southwards and westwards wintering in Ireland, France and Iberia (Hudson *et al.* 1994). Within the EU, hunting of Northern Lapwing is legal only in France, Greece, Italy and Spain (Trolliet 2003). It is feasible that birds breeding in the more southerly latitudes of Wales over-winter in Europe and therefore may face higher rates of over-winter mortality through hunting pressure. However, regional survival rates and philopatry have not been studied such a spatial scale that would allow detection of any such variations.

Although there is general agreement that Northern Lapwing declines have been driven primarily by agricultural change (Baines 1990; Chamberlain *et al.* 2001; Stephens *et al.* 2003), due to their diminished breeding densities and/or habitat fragmentation, Northern Lapwing populations may now be more vulnerable to the attentions of predators (the so-called "predator trap hypothesis", Newton 1998; Evans 2004). In addition, the populations of some predators, such as Carrion Crows have increased in recent decades (Gregory & Marchant 1995), although the national population trends of Foxes (*Vulpes vulpes)* are less certain (Tapper 1992; Reynolds & Tapper 1994; Harris *et al.* 1995; Webbon *et al.* 2004). Taken together, it is perhaps not surprising that a recent analysis of Northern Lapwing nest record card data (Chamberlain & Crick 2003) found that proportion of nest failures reported due to predation has increased during the 1990s.

Whilst impact of predators on nest survival is relatively simple to quantify from field signs (although identifying predator species responsible is more difficult), quantifying the impact of predators on chick survival presents a far greater challenge. Yet in demographic terms chick survival is likely to be of greater importance in determining annual productivity than is nest survival, since chick losses are only rarely followed by re-nesting, whereas females may lay up to four replacement clutches following nest loss (Klomp 1951). The three principal proximate causes of chick mortality are adverse weather conditions, insufficient food availability and predation (Trolliet 2003, see also Chapter 5). Clearly these three factors are likely to interact (deterioration in habitat quality may result in under-nourishment of chicks due to low food availability, making them more vulnerable to adverse weather, and also more vulnerable to predators). Teasing apart proximate from ultimate causation of chick mortality, and devising effective habitat modifications at the appropriate spatial scale, within the context of an agri-environment framework is the challenge that lies ahead.

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Appendix

Year	Site	Grid Reference	Latitude	Longitude	Site area (ha)	Reserve	Breeding pairs	Number of fledged chicks	Habitat code	Management codes
1998	Cors Crugyll	SH334764	53.258	-4.497	34	yes	1		3	1
1999	Cors Crugyll	SH334765	53.258	-4.497	34	yes	3		3	2
2000	Cors Crugyll	SH334766	53.258	-4.497	34	yes	9	1	3	2
2001	Cors Crugyll	SH334767	53.258	-4.497	34	yes	9		3	1
2002	Cors Crugyll	SH334768	53.258	-4.497	34	yes	10		3	1
2003	Cors Crugyll	SH334769	53.258	-4.497	34	yes	9		3	1
1998	Plas Bog	SH338768	53.262	-4.492	54.56	yes	1		6	4
1999	Plas Bog	SH338769	53.262	-3.492	54.56	yes	1		6	1
2000	Plas Bog	SH338770	53.262	-2.492	54.56	yes	0		6	2
2001	Plas Bog	SH338771	53.262	-1.492	54.56	yes	0		6	2
2002	Plas Bog	SH338772	53.262	-0.492	54.56	yes	1		6	1
2003	Plas Bog	SH338773	53.262	0.508	54.56	yes	1		6	1
1998	Dinas Dinlle	SH435602	53.116	-4.338	431.6	no	28	1	5	0
1999	Dinas Dinlle	SH435603	53.116	-4.338	431.6	no	28	1	5	0
2000	Dinas Dinlle	SH435604	53.116	-4.338	431.6	no	23	1	5	0
2001	Dinas Dinlle	SH435605	53.116	-4.338	431.6	no			5	0
2002	Dinas Dinlle	SH435606	53.116	-4.338	431.6	no	4	1	5	0
2003	Dinas Dinlle	SH435607	53.116	-4.338	431.6	no	6	0	5	0
1998	Malltraeth	SH452718	53.220	-4.319	27	yes	1	1	3	1
1999	Malltraeth	SH452719	53.220	-4.319	27	yes	3	1	3	1
2000	Malltraeth	SH452720	53.220	-4.319	27	yes	6	1	3	1
2001	Malltraeth	SH452721	53.220	-4.319	27	yes	5		3	1
2002	Malltraeth	SH452722	53.220	-4.319	27	yes	10		3	1
2003	Malltraeth	SH452723	53.220	-4.319	27	yes	13		3	1
1998	Ystymllun	SH522385	52.923	-4.198	13	no	0	0	3	0
1999	Ystymllun	SH522386	52.923	-4.198	13	no	0	0	3	0
2000	Ystymllun	SH522387	52.923	-4.198	13	no	10	0	3	0
2001	Ystymllun	SH522388	52.923	-4.198	13	no			3	0

2002	Ystymllun	SH522389	52.923	-4.198	13	no			3	0
2003	Ystymllun	SH522390	52.923	-4.198	13	no			3	0
1998	Morfa Harlech	SH570350	52.893	-4.126	150.08	no	18		3	1
1999	Morfa Harlech	SH570351	52.893	-4.126	150.08	no	12		3	1
2000	Morfa Harlech	SH570352	52.893	-4.126	150.08	no	15		3	1
2001	Morfa Harlech	SH570353	52.893	-4.126	150.08	no			3	1
2002	Morfa Harlech	SH570354	52.893	-4.126	150.08	no			3	1
2003	Morfa Harlech	SH570355	52.893	-4.126	150.08	no	21.5	0	3	1
1998	Madryn	SH664741	53.247	-4.002	16	no	21	1	6	4
1999	Madryn	SH664742	53.247	-4.002	16	no	21	1	6	2
2000	Madryn	SH664743	53.247	-4.002	16	no	18	1	6	2
2001	Madryn	SH664744	53.247	-4.002	16	no			6	2
2002	Madryn	SH664745	53.247	-4.002	16	no			6	
2003	Madryn	SH664746	53.247	-4.002	16	no			6	
1998	Tremorfa	SH793729	53.239	-3.809	21	no	15	1	5	4
1999	Tremorfa	SH793730	53.239	-3.809	21	no	14	1	5	4
2000	Tremorfa	SH793731	53.239	-3.809	21	no	11	1	5	4
2001	Tremorfa	SH793732	53.239	-3.809	21	no			5	4
2002	Tremorfa	SH793733	53.239	-3.809	21	no			5	2
2003	Tremorfa	SH793734	53.239	-3.809	21	no			5	2
1998	Conwy RSPB	SH800770	53.276	-3.800	47	yes	12	1	3	1
1999	Conwy RSPB	SH800771	53.276	-3.800	47	yes	9	1	3	1
2000	Conwy RSPB	SH800772	53.276	-3.800	47	yes	13	1	3	1
2001	Conwy RSPB	SH800773	53.276	-3.800	47	yes			3	1
2002	Conwy RSPB	SH800774	53.276	-3.800	47	yes			3	1
2003	Conwy RSPB	SH800775	53.276	-3.800	47	yes			3	2
1998	Bodafon Fields	SH802820	53.321	-3.798	8.6	no	4	1	1	0
1999	Bodafon Fields	SH802821	53.321	-3.798	8.6	no	3	1	1	0
2000	Bodafon Fields	SH802822	53.321	-3.798	8.6	no	4	0	1	0
2001	Bodafon Fields	SH802823	53.321	-3.798	8.6	no			1	0
2002	Bodafon Fields	SH802824	53.321	-3.798	8.6	no			1	0
2003	Bodafon Fields	SH802825	53.321	-3.798	8.6	no	2		1	0
1998	Penrhyn Bay	SH827807	53.310	-3.760	33	no	3	1	1	0
1999	Penrhyn Bay	SH827808	53.310	-3.760	33	no	9	1	1	0
2000	Penrhyn Bay	SH827809	53.310	-3.760	33	no	10	1	1	0

2001	Penrhyn Bay	SH827810	53.310	-3.760	33	no			1	0
2002	Penrhyn Bay	SH827811	53.310	-3.760	33	no			1	0
2003	Penrhyn Bay	SH827812	53.310	-3.760	33	no			1	0
1998	Banhadla Farm	SJ167244	52.810	-3.236	45	no	5		4	0
1999	Banhadla Farm	SJ167245	52.810	-3.236	45	no	10		4	0
2000	Banhadla Farm	SJ167246	52.810	-3.236	45	no	3	1	4	0
2001	Banhadla Farm	SJ167247	52.810	-3.236	45	no			4	0
2002	Banhadla Farm	SJ167248	52.810	-3.236	45	no			4	0
2003	Banhadla Farm	SJ167249	52.810	-3.236	45	no			4	0
1998	Sealand Ranges	SJ302730	53.249	-3.046	27.7	no	12	1	3	0
1999	Sealand Ranges	SJ302731	53.249	-3.046	27.7	no	22	1	3	0
2000	Sealand Ranges	SJ302732	53.249	-3.046	27.7	no	25	1	3	0
2001	Sealand Ranges	SJ302733	53.249	-3.046	27.7	no	13		3	0
2002	Sealand Ranges	SJ302734	53.249	-3.046	27.7	no	11.5		3	0
2003	Sealand Ranges	SJ302735	53.249	-3.046	27.7	no	19	0	3	0
1998	Inner Marsh Farm & Shotwick	SJ313731	53.250	-3.030	181.37	no	48.5	1	6	4
1999	Inner Marsh Farm & Shotwick	SJ313732	53.250	-3.030	181.37	no	42.5	1	6	1
2000	Inner Marsh Farm & Shotwick	SJ313733	53.250	-3.030	181.37	no	30.5	1	6	2
2001	Inner Marsh Farm & Shotwick	SJ313734	53.250	-3.030	181.37	no			6	2
2002	Inner Marsh Farm & Shotwick	SJ313735	53.250	-3.030	181.37	no			6	2
2003	Inner Marsh Farm & Shotwick	SJ313736	53.250	-3.030	181.37	no	37	0	6	2
1998	Beeches Farm	SJ347663	53.189	-2.977	147.03	no	55.5	1	6	1
1999	Beeches Farm	SJ347664	53.189	-2.977	147.03	no	53.5	1	6	1
2000	Beeches Farm	SJ347665	53.189	-2.977	147.03	no	55	1	6	1
2001	Beeches Farm	SJ347666	53.189	-2.977	147.03	no			6	1
2002	Beeches Farm	SJ347667	53.189	-2.977	147.03	no	44.5	1	6	1
2003	Beeches Farm	SJ347668	53.189	-2.977	147.03	no	35	1	6	2
1998	Hawarden Airfield	SJ349652	53.179	-2.974	119.16	no	13		1	0
1999	Hawarden Airfield	SJ349653	53.179	-2.974	119.16	no	10		1	0
2000	Hawarden Airfield	SJ349654	53.179	-2.974	119.16	no	5		1	0
2001	Hawarden Airfield	SJ349655	53.179	-2.974	119.16	no			1	0
2002	Hawarden Airfield	SJ349656	53.179	-2.974	119.16	no			1	0
2003	Hawarden Airfield	SJ349657	53.179	-2.974	119.16	no			1	0
1998	Burton Meadows	SJ355602	53.135	-2.964	32.25	no			4	0

1999	Burton Meadows	SJ355603	53.135	-2.964	32.25	no	20	1	4	0
2000	Burton Meadows	SJ355604	53.135	-2.964	32.25	no	50	1	4	0
2001	Burton Meadows	SJ355605	53.135	-2.964	32.25	no			4	0
2002	Burton Meadows	SJ355606	53.135	-2.964	32.25	no	15	1	4	0
2003	Burton Meadows	SJ355607	53.135	-2.964	32.25	no	5.5	0	4	0
1998	Pulford & Trevalyn Meadows	SJ391569	53.105	-2.910	197	no	8		6	0
1999	Pulford & Trevalyn Meadows	SJ391570	53.105	-2.910	197	no	27	1	6	0
2000	Pulford & Trevalyn Meadows	SJ391571	53.105	-2.910	197	no	18.5	1	6	0
2001	Pulford & Trevalyn Meadows	SJ391572	53.105	-2.910	197	no			6	0
2002	Pulford & Trevalyn Meadows	SJ391573	53.105	-2.910	197	no	12	1	6	0
2003	Pulford & Trevalyn Meadows	SJ391574	53.105	-2.910	197	no	9		6	0
1998	Holt (Wrexham)	SJ410525	53.066	-2.880	83.75	no	13		6	0
1999	Holt (Wrexham)	SJ410526	53.066	-2.880	83.75	no	20	1	6	0
2000	Holt (Wrexham)	SJ410527	53.066	-2.880	83.75	no	11	1	6	0
2001	Holt (Wrexham)	SJ410528	53.066	-2.880	83.75	no			6	0
2002	Holt (Wrexham)	SJ410529	53.066	-2.880	83.75	no			6	0
2003	Holt (Wrexham)	SJ410530	53.066	-2.880	83.75	no	9.5		6	0
1998	Ramsey Island	SM700237	51.864	-5.340	107	yes	13	1	3	4
1999	Ramsey Island	SM700238	51.864	-5.340	107	yes	13	1	3	1
2000	Ramsey Island	SM700239	51.864	-5.340	107	yes	7	1	3	3
2001	Ramsey Island	SM700240	51.864	-5.340	107	yes	10	1	3	3
2002	Ramsey Island	SM700241	51.864	-5.340	107	yes	9	1	3	1
2003	Ramsey Island	SM700242	51.864	-5.340	107	yes	8	1	3	1
1998	Cefngwyn Hall	SN530646	52.259	-4.154	9	no			6	2
1999	Cefngwyn Hall	SN530647	52.259	-4.154	9	no	0		6	2
2000	Cefngwyn Hall	SN530648	52.259	-4.154	9	no	3	1	6	2
2001	Cefngwyn Hall	SN530649	52.259	-4.154	9	no	6	1	6	2
2002	Cefngwyn Hall	SN530650	52.259	-4.154	9	no			6	2
2003	Cefngwyn Hall	SN530651	52.259	-4.154	9	no			6	2
1998	Penllyn	SN590982	52.563	-4.080	70.969	no	8	1	5	4
1999	Penllyn	SN590983	52.563	-4.080	70.969	no	13	1	5	2
2000	Penllyn	SN590984	52.563	-4.080	70.969	no	22	1	5	2
2001	Penllyn	SN590985	52.563	-4.080	70.969	no	20		5	2
2002	Penllyn	SN590986	52.563	-4.080	70.969	no	19	1	5	2

2003	Penllyn	SN590987	52.563	-4.080	70.969	no	8	1	5	2
1998	Aber Leri	SN613918	52.506	-4.043	64.109	yes	1	0	5	2
1999	Aber Leri	SN613919	52.506	-4.043	64.109	yes	1	0	5	2
2000	Aber Leri	SN613920	52.506	-4.043	64.109	yes	5	1	5	1
2001	Aber Leri	SN613921	52.506	-4.043	64.109	yes	3		5	3
2002	Aber Leri	SN613922	52.506	-4.043	64.109	yes	12	1	5	2
2003	Aber Leri	SN613923	52.506	-4.043	64.109	yes	6	1	5	2
1998	Lodge Park	SN650940	52.526	-3.990	60.185	no	11	1	5	2
1999	Lodge Park	SN650941	52.526	-3.990	60.185	no	7	1	5	2
2000	Lodge Park	SN650942	52.526	-3.990	60.185	no	10	1	5	2
2001	Lodge Park	SN650943	52.526	-3.990	60.185	no	6	0	5	2
2002	Lodge Park	SN650944	52.526	-3.990	60.185	no	4	1	5	2
2003	Lodge Park	SN650945	52.526	-3.990	60.185	no	14	1	5	2
1998	Hen Hafod	SN658948	52.534	-3.978	96.6	no	22		1	0
1999	Hen Hafod	SN658949	52.534	-3.978	96.6	no	18		1	0
2000	Hen Hafod	SN658950	52.534	-3.978	96.6	no	28		1	0
2001	Hen Hafod	SN658951	52.534	-3.978	96.6	no	26		1	0
2002	Hen Hafod	SN658952	52.534	-3.978	96.6	no	18		1	0
2003	Hen Hafod	SN658953	52.534	-3.978	96.6	no			1	0
1998	Penrhyngerwyn	SN665953	52.539	-3.968	87	no	20		2	4
1999	Penrhyngerwyn	SN665954	52.539	-3.968	87	no	21	1	2	4
2000	Penrhyngerwyn	SN665955	52.539	-3.968	87	no	5		2	4
2001	Penrhyngerwyn	SN665956	52.539	-3.968	87	no	5		2	4
2002	Penrhyngerwyn	SN665957	52.539	-3.968	87	no	19		2	2
2003	Penrhyngerwyn	SN665958	52.539	-3.968	87	no	37	1	2	2
1998	Cors Caron NNR	SN673621	52.240	-3.943	15	yes	1	0	3	4
1999	Cors Caron NNR	SN673622	52.240	-3.943	15	yes	1	0	3	4
2000	Cors Caron NNR	SN673623	52.240	-3.943	15	yes	7	0	3	4
2001	Cors Caron NNR	SN673624	52.240	-3.943	15	yes	5	1	3	1
2002	Cors Caron NNR	SN673625	52.240	-3.943	15	yes	5	0	3	1
2003	Cors Caron NNR	SN673626	52.240	-3.943	15	yes	13	0	3	1
1998	Cors Penbwlch, Ystrad Meurig	SN680687	52.300	-3.936	13.43	no	10	1	3	0
1999	Cors Penbwlch, Ystrad Meurig	SN680688	52.300	-3.936	13.43	no	4	1	3	0
2000	Cors Penbwlch, Ystrad Meurig	SN680689	52.300	-3.936	13.43	no	2	0	3	0
2001	Cors Penbwlch, Ystrad Meurig	SN680690	52.300	-3.936	13.43	no			3	0

2002	Cors Penbwlch, Ystrad Meurig	SN680691	52.300	-3.936	13.43	no			3	0
2003	Cors Penbwlch, Ystrad Meurig	SN680692	52.300	-3.936	13.43	no	0	0	3	0
1998	Penmaen Isaf (LWG)	SN680979	52.562	-3.947	21.358	no	12	1	5	2
1999	Penmaen Isaf (LWG)	SN680980	52.562	-3.947	21.358	no	9	1	5	2
2000	Penmaen Isaf (LWG)	SN680981	52.562	-3.947	21.358	no	23	1	5	1
2001	Penmaen Isaf (LWG)	SN680982	52.562	-3.947	21.358	no	23		5	2
2002	Penmaen Isaf (LWG)	SN680983	52.562	-3.947	21.358	no	14	1	5	1
2003	Penmaen Isaf (LWG)	SN680984	52.562	-3.947	21.358	no	5	0	5	1
1998	Ynys-hir	SN685966	52.551	-3.939	16.682	yes	14	1	3	1
1999	Ynys-hir	SN685967	52.551	-3.939	16.682	yes	24	1	3	1
2000	Ynys-hir	SN685968	52.551	-3.939	16.682	yes	7	0	3	2
2001	Ynys-hir	SN685969	52.551	-3.939	16.682	yes	6		3	2
2002	Ynys-hir	SN685970	52.551	-3.939	16.682	yes	0	0	3	2
2003	Ynys-hir	SN685971	52.551	-3.939	16.682	yes	2	0	3	2
1998	Roman Road, Trecastle	SN837298	51.954	-3.692	14.3	no			3	0
1999	Roman Road, Trecastle	SN837299	51.954	-3.692	14.3	no			3	0
2000	Roman Road, Trecastle	SN837300	51.954	-3.692	14.3	no	7	1	3	0
2001	Roman Road, Trecastle	SN837301	51.954	-3.692	14.3	no			3	0
2002	Roman Road, Trecastle	SN837302	51.954	-3.692	14.3	no	5	1	3	0
2003	Roman Road, Trecastle	SN837303	51.954	-3.692	14.3	no	5		3	0
1998	Mynydd Illtyd	SN968255	51.918	-3.500	40	no	12		3	4
1999	Mynydd Illtyd	SN968256	51.918	-3.500	40	no	10	1	3	4
2000	Mynydd Illtyd	SN968257	51.918	-3.500	40	no	7	1	3	4
2001	Mynydd Illtyd	SN968258	51.918	-3.500	40	no	1		3	1
2002	Mynydd Illtyd	SN968259	51.918	-3.500	40	no	1	0	3	1
2003	Mynydd Illtyd	SN968260	51.918	-3.500	40	no	0	0	3	1
1998	Pant y Dwr, Rhosgoch	SN991775	52.386	-3.482	5	no	10		3	4
1999	Pant y Dwr, Rhosgoch	SN991776	52.386	-3.482	5	no	8	1	3	4
2000	Pant y Dwr, Rhosgoch	SN991777	52.386	-3.482	5	no	9	0	3	4
2001	Pant y Dwr, Rhosgoch	SN991778	52.386	-3.482	5	no			3	1
2002	Pant y Dwr, Rhosgoch	SN991779	52.386	-3.482	5	no	2.5	0	3	3
2003	Pant y Dwr, Rhosgoch	SN991780	52.386	-3.482	5	no	0	0	3	3
1998	Dyfnant	SO025505	52.143	-3.425	12	no	8	1	5	1
1999	Dyfnant	SO025506	52.143	-3.425	12	no	1	0	5	1

2000	Dyfnant	SO025507	52.143	-3.425	12	no	4	0	5	1
2001	Dyfnant	SO025508	52.143	-3.425	12	no			5	1
2002	Dyfnant	SO025509	52.143	-3.425	12	no	0	0	5	1
2003	Dyfnant	SO025510	52.143	-3.425	12	no	0	0	5	1
1998	Fochriw	SO096060	51.745	-3.309	35	no	17	1	3	1
1999	Fochriw	SO096061	51.745	-3.309	35	no	17	1	3	3
2000	Fochriw	SO096062	51.745	-3.309	35	no	33	1	3	3
2001	Fochriw	SO096063	51.745	-3.309	35	no	28		3	1
2002	Fochriw	SO096064	51.745	-3.309	35	no	9	1	3	1
2003	Fochriw	SO096065	51.745	-3.309	35	no			3	1
1998	Llangasty,Llangorse	SO134262	51.927	-3.259	24.6	no	7	1	3	1
1999	Llangasty,Llangorse	SO134263	51.927	-3.259	24.6	no	7	1	3	1
2000	Llangasty,Llangorse	SO134264	51.927	-3.259	24.6	no	7	1	3	1
2001	Llangasty,Llangorse	SO134265	51.927	-3.259	24.6	no			3	1
2002	Llangasty,Llangorse	SO134266	51.927	-3.259	24.6	no	4	1	3	1
2003	Llangasty,Llangorse	SO134267	51.927	-3.259	24.6	no	2		3	1
1998	Rhyd y Blew	SO155114	51.794	-3.225	23.5	no	16	0	3	4
1999	Rhyd y Blew	SO155115	51.794	-3.225	23.5	no	0		3	4
2000	Rhyd y Blew	SO155116	51.794	-3.225	23.5	no	7	1	3	4
2001	Rhyd y Blew	SO155117	51.794	-3.225	23.5	no	13		3	1
2002	Rhyd y Blew	SO155118	51.794	-3.225	23.5	no			3	3
2003	Rhyd y Blew	SO155119	51.794	-3.225	23.5	no	2	0	3	3
1998	Cefn Manmoel	SO172058	51.744	-3.199	31.4	no	12		3	0
1999	Cefn Manmoel	SO172059	51.744	-3.199	31.4	no	3		3	0
2000	Cefn Manmoel	SO172060	51.744	-3.199	31.4	no	0	0	3	0
2001	Cefn Manmoel	SO172061	51.744	-3.199	31.4	no			3	0
2002	Cefn Manmoel	SO172062	51.744	-3.199	31.4	no			3	0
2003	Cefn Manmoel	SO172063	51.744	-3.199	31.4	no			3	0
1998	Kays & Kears, Blaenavon	SO238097	51.780	-3.104	11.1	no	4		3	0
1999	Kays & Kears, Blaenavon	SO238098	51.780	-3.104	11.1	no	4		3	0
2000	Kays & Kears, Blaenavon	SO238099	51.780	-3.104	11.1	no	4		3	0

2001	Kays & Kears, Blaenavon	SO238100	51.780	-3.104	11.1	no	0		3	0
2002	Kays & Kears, Blaenavon	SO238101	51.780	-3.104	11.1	no			3	0
2003	Kays & Kears, Blaenavon	SO238102	51.780	-3.104	11.1	no	0	0	3	0
1998	Castlemartin Range	SR930950	51.615	-4.990	30	no	10	1	3	0
1999	Castlemartin Range	SR930951	51.615	-4.990	30	no	1	1	3	0
2000	Castlemartin Range	SR930952	51.615	-4.990	30	no	4		3	0
2001	Castlemartin Range	SR930953	51.615	-4.990	30	no	0		3	0
2002	Castlemartin Range	SR930954	51.615	-4.990	30	no	0		3	0
2003	Castlemartin Range	SR930955	51.615	-4.990	30	no	0		3	0
1998	Penclacwydd	SS532984	51.664	-4.122	28.86	yes	22		6	2
1999	Penclacwydd	SS532985	51.664	-4.122	28.86	yes	28	1	6	2
2000	Penclacwydd	SS532986	51.664	-4.122	28.86	yes	28	1	6	2
2001	Penclacwydd	SS532987	51.664	-4.122	28.86	yes	16		6	2
2002	Penclacwydd	SS532988	51.664	-4.122	28.86	yes			6	2
2003	Penclacwydd	SS532989	51.664	-4.122	28.86	yes			6	2
1998	Llandarcy	SS718960	51.647	-3.853	2	no			3	0
1999	Llandarcy	SS718961	51.647	-3.853	2	no	5	1	3	0
2000	Llandarcy	SS718962	51.647	-3.853	2	no	6		3	0
2001	Llandarcy	SS718963	51.647	-3.853	2	no	1		3	0
2002	Llandarcy	SS718964	51.647	-3.853	2	no			3	0
2003	Llandarcy	SS718965	51.647	-3.853	2	no			3	0
1998	Baglan Energy Park	SS732930	51.621	-3.831	95	no			3	0
1999	Baglan Energy Park	SS732931	51.621	-3.831	95	no	10		3	0
2000	Baglan Energy Park	SS732932	51.621	-3.831	95	no	5		3	0
2001	Baglan Energy Park	SS732933	51.621	-3.831	95	no	10		3	0
2002	Baglan Energy Park	SS732934	51.621	-3.831	95	no			3	0
2003	Baglan Energy Park	SS732935	51.621	-3.831	95	no			3	0
1998	Baglan Moors,Panasonic	SS750915	51.608	-3.805	10.6	no	9	1	3	4
1999	Baglan Moors,Panasonic	SS750916	51.608	-3.805	10.6	no	8	1	3	4
2000	Baglan Moors,Panasonic	SS750917	51.608	-3.805	10.6	no	5	1	3	4
2001	Baglan Moors,Panasonic	SS750918	51.608	-3.805	10.6	no	5		3	4
2002	Baglan Moors,Panasonic	SS750919	51.608	-3.805	10.6	no	5		3	1
2003	Baglan Moors,Panasonic	SS750920	51.608	-3.805	10.6	no	5		3	1
1998	Junct 37 M4	SS829814	51.518	-3.687	12	no			2	0

1999	Junct 37 M5	SS829815	51.518	-3.687	12	no	3		2	0
2000	Junct 37 M6	SS829816	51.518	-3.687	12	no	5	1	2	0
2001	Junct 37 M7	SS829817	51.518	-3.687	12	no	3		2	0
2002	Junct 37 M8	SS829818	51.518	-3.687	12	no			2	0
2003	Junct 37 M9	SS829819	51.518	-3.687	12	no			2	0
1998	Parc Slip	SS875839	51.542	-3.622	11.5	yes	16	1	3	4
1999	Parc Slip	SS875840	51.542	-3.622	11.5	yes	8	0	3	4
2000	Parc Slip	SS875841	51.542	-3.622	11.5	yes	8	0	3	2
2001	Parc Slip	SS875842	51.542	-3.622	11.5	yes	13		3	1
2002	Parc Slip	SS875843	51.542	-3.622	11.5	yes	3		3	1
2003	Parc Slip	SS875844	51.542	-3.622	11.5	yes	9		3	1
1998	Tyle Coch	SS888876	51.575	-3.604	19.5	no	6		3	0
1999	Tyle Coch	SS888877	51.575	-3.604	19.5	no	8	1	3	0
2000	Tyle Coch	SS888878	51.575	-3.604	19.5	no	8	0	3	0
2001	Tyle Coch	SS888879	51.575	-3.604	19.5	no	6		3	0
2002	Tyle Coch	SS888880	51.575	-3.604	19.5	no	8	0	3	0
2003	Tyle Coch	SS888881	51.575	-3.604	19.5	no	0.5	0	3	0
1998	Newton Farm, Gwent Levels	ST237787	51.501	-3.099	15	no			4	0
1999	Newton Farm, Gwent Levels	ST237788	51.501	-3.099	15	no	6	1	4	0
2000	Newton Farm, Gwent Levels	ST237789	51.501	-3.099	15	no	4	1	4	0
2001	Newton Farm, Gwent Levels	ST237790	51.501	-3.099	15	no			4	0
2002	Newton Farm, Gwent Levels	ST237791	51.501	-3.099	15	no	3	1	4	0
2003	Newton Farm, Gwent Levels	ST237792	51.501	-3.099	15	no			4	0
1998	Tregrug Farm	ST380972	51.669	-2.896	75.8	no	20		4	4
1999	Tregrug Farm	ST380973	51.669	-2.896	75.8	no	20		4	4
2000	Tregrug Farm	ST380974	51.669	-2.896	75.8	no	25	1	4	1
2001	Tregrug Farm	ST380975	51.669	-2.896	75.8	no			4	1
2002	Tregrug Farm	ST380976	51.669	-2.896	75.8	no	3.5	1	4	3
2003	Tregrug Farm	ST380977	51.669	-2.896	75.8	no			4	3

Habitat codes: 1=improved grass, 2=arable, 3=extensive grass, 4=improved grass + arable, 5=improved + extensive grass, 6=arable + extensive grass.
Management codes: 0=not managed, 1=part-managed, 2=fully managed, 3=post management, 4=prior management.

Lapwing breeding densities

Full model:

Effect	D.F.	F statistic	P-value
Year	1,59.3	3.11	0.0828
Management	4,67.9	0.47	0.7570
Latitude	1,37	0.60	0.4440
Reserve	1,41.7	3.40	0.0725
Habitat	4,34.3	1.19	0.3313
Wet features	1,21.3	1.17	0.2907
Livestock	3,61.4	0.57	0.6387
Predator density	1,70.8	0.56	0.4574
Year*Reserve	1,61.2	0.88	0.3520
Year*Latitude	1,59.4	3.01	0.0877
Predator density*Habitat	4,70.8	1.21	0.3154
Predator density*Management	4,67.3	0.55	0.6968

Minimal model:

Effect	Estimate	Standard Error	D.F.	F statistic	P-value
Intercept	24.7105	11.9810	74.3		
Year	-4.6531	2.0096	1,178	5.49	0.0202
Latitude	-0.5007	0.2283	1,74.7	4.81	0.0314
Reserve	0.5852	0.3726	1,79.1	2.47	0.1203
Year*Reserve	-0.1461	0.06031	1,178	5.87	0.0164
Year*Latitude	0.08913	0.03838	1,178	5.39	0.0213
Terms dropped					
Management			4,169	1.45	0.2193
Predator density			1,96.6	0.04	0.8442
Wet features			1,45	1.42	0.2398
Habitat			4,41.8	0.38	0.8629
Livestock			1,158	0.82	0.4848
Predator density*Habitat			4,87.5	0.80	0.5313
Predator density*Management			4,82.7	0.62	0.6526

Lapwing productivity

Full model:

Effect	D.F	F statistic	P-value
Management	4,32	1.75	0.1624
Reserve	1,45.8	0.04	0.8373
Habitat	4,30.1	0.26	0.9026
Wet features	1,20.2	2.28	0.1462
Livestock	1,24.6	0.77	0.5192
Year	5,52	1.80	0.1427
Predator density	1,52.8	0.08	0.7775
Latitude	1,39.4	3.05	0.0886
Reserve*Year	5,51.5	1.03	0.3999
Latitude*Year	5,52	1.80	0.1431
Predator density*Habitat	4,27.8	0.62	0.6550
Predator density*Management	4,41.3	0.47	0.7608

Minimal model:

Effect	Estimate	Standard Error	D.F.	F statistic	P-value
Intercept	21.2960	7.6842	38.8		
Year			5,124	5.44	0.0001

1998	0.7561	0.3493			
1999	1.2276	0.3284			
2000	0.6324	0.3397			
2001	1.1742	0.5082			
2002	0.3642	0.4059			
2003	0	.			
Latitude	-0.4411	0.1461	1,38.4	9.12	0.0045
Terms dropped					
Management			4,86.3	1.41	0.2358
Reserve			1,36.7	1.30	0.2621
Habitat			5,40.1	0.79	0.5642
Wet features			1,40	0.84	0.3653
Livestock			1,69.2	0.92	0.4351
Predator density			1,45.2	1.02	0.3055
Reserve*Year			5,116	1.46	0.2088
Latitude*Year			5,118	0.66	0.6515
Predator density*Habitat			4,49.3	0.51	0.7310
Predator density*Management			4,70.3	0.99	0.4194

Chapter 3.

Remote monitoring of Northern Lapwing nests using digital camera technology

Fiona Sharpe, Mark Bolton and Nigel Butcher

Abstract

Remote nest cameras have been deployed for many years for the collection of scientific data. These systems have traditionally been expensive, bulky, heavy and power-hungry and required considerable ongoing maintenance. Digital camera technology has developed extremely rapidly in the last few years and this has led to a vast increase in image storage capacity, coupled with a reduction in power consumption. The advent of digital technology and sophisticated triggering mechanisms such as Video Motion Detection heralds a new era of lower-cost, small, lightweight, energy-efficient systems, requiring less frequent maintenance. Here we describe a design of remote digital camera which has been successfully employed to monitor predation events at Northern Lapwing (*Vanellus vanellus*) nests. For such an application, the system autonomy is not constrained by image storage capacity, since storage cards have extremely high capacity; they can be configured to overwrite once full, and following a nest predation event, further image capture is low. In this case, autonomy is governed by power consumption. We trialled three system configurations to reduce power requirements, without compromising predation-event recording capability. We found that the use of passive infra-red sensor trigger to awake the system from standby mode did not compromise reliability, and substantially reduced power consumption. On this system a 38 Ahr battery provided a field autonomy of approximately five days. Larger-scale deployment of this system is planned for monitoring wader nest predation on RSPB reserves and further, simple modifications would allow the system to be adapted for a wide range of scientific and nest surveillance operations.

Introduction

Nest predation is a primary cause of nest failure for many bird species (Ricklefs 1969) and is one the major selective agents shaping avian life histories. Many bird species that breed on farmland and remaining woodland patches are declining (Gregory *et al.* 2004), and some of these declines may be due to increased predation (Newton 2004). Ground-nesting birds, such as Northern Lapwings *Vanellus vanellus* are particularly vulnerable to nest predation from both avian and mammalian predators. Northern Lapwing populations are declining in a number of northern European countries (Wilson *et al.* 2001; Trolliet 2003; BirdLife International 2004). In the United Kingdom (UK) Northern Lapwings have undergone a marked decline in breeding numbers and a contraction in range between 1970 and 1990 (Gibbons *et al.* 1993) and this decline has continued over recent decades with an estimated decrease of 49% between 1987 and 1998 (Wilson *et al.* 2001). Although there are a number of potential factors that may be driving this population decline including major changes in modern farming practices (Chamberlain & Fuller 2000; Chamberlain *et al.* 2000; Donald *et al.* 2001), recent evidence suggests that recent changes in population size may have been influenced by changes in clutch failure rates, which may have been mediated by increased predation rates (Chamberlain & Crick 2003).

If conservation initiatives are to be successful at halting the decline of breeding Northern Lapwings in the UK and the rest of Europe, it is necessary that nest predators are correctly identified so that problem of nest predation can be tackled effectively.

Methods for monitoring nest predation.

A wide variety of methods and techniques have been employed to identify nest predators. These methods can be indirect, for example, the examination of egg shell remains (Green *et al.* 1987) and the use of temperature data loggers in nests to determine the timing of predation events by quantifying incubation patterns and nest attendance (Flint & MacCluskie 1995; Joyce *et al.* 2001), or direct identification of nest predators using nest cameras (Picman & Schriml 1994; Danielson *et al.* 1996; Pietz & Granfors 2000; Booms & Fuller 2003; Renfrew & Ribic 2003; Sawin *et al.* 2003; Thompson & Burhans 2003; Anthony *et al.* 2004).

The examination of eggshell remnants can yield some information as to the identity of egg predators (Green *et al.* 1987). However, there are many problems associated with identifying nest predators from nest remains (Larivière 1999) and different predator species may differ in their tendency to leave traces in the vicinity of the nest (Green *et al.* 1987), for example in the case of Northern Lapwings, the tendency of Northern Lapwings to vigorously attack egg predators often causes Carrion Crows *Corvus corvus corone* to carry eggs out of the range of the attacking adults before consuming them (Green *et al.* 1987; personal observation). Therefore, the identification of nest predators through eggshell remnants alone may place the blame on the wrong species having serious and expensive implications in wildlife management (Larivière 1999).

Remote monitoring of avian nests is routinely undertaken for a wide range of scientific, educational and conservation-surveillance purposes. Data-logging thermistor probes located in the nest cup can provide useful information regarding the time of day nests are depredated (Flint & MacCluskie 1995; Joyce *et al.* 2001), but cannot indicate the precise predator species involved. In the case of Northern Lapwings, temperature profiles also need to be interpreted with care, since adults may return to incubate the empty nest for some hours after a predation event (personal observation).

Image-capture devices, such as video and stills cameras have been deployed with great success and offer indisputable evidence of nest predator identification. The types of image-capture systems used vary from simple setups of adapted 35mm cameras linked to triggers which activate the shutter and a photograph is taken (Picman & Schriml 1994; Danielson *et al.* 1996; Sawin *et al.* 2003; Anthony *et al.* 2004) to time-lapse video recorders (Pietz & Granfors 2000; Booms & Fuller 2003; Renfrew & Rubic 2003; Thompson & Burhans 2003). Time-lapse video recorders have the advantage of not relying on any triggering system so the chances of missing a predation event are small. However, they are often large, expensive and require frequent ongoing maintenance (e.g. replacement of batteries and film) that can limit simultaneous deployment of multiple units necessary to obtain large sample sizes. In 2003 the Royal Society for the Protection of Bids (RSPB) developed an analogue recording system to monitor Northern Lapwing nest predation, based on a time lapse VHS recorder. Rather than have cables run across a field increasing the risk of

predation, the picture was transmitted by microwave (2.4GHz) to a recording box. This was positioned around 100 metres from the nest located at the field boundary. A small black and white camera with controlled infrared illumination was located close to the nest. This was connected to a battery that provided power for the period of a week. The time lapse recorder was housed in a container the size of a large suitcase with a large 12V 38Ah battery to power which required replacement every 24 hours. Although a small amount of valuable information was obtained, the system demanded a high degree of maintenance (daily replacement of 12V battery and VHS cassette) and the simultaneous deployment of multiple units would have been impractical in most field situations. Whilst this system was capable of successfully identifying nest predators, there is clearly still a need for relatively inexpensive, lightweight, reliable systems with a high degree of field autonomy. Recent advances in digital camera technology have made such devices possible and the aim of this study was to field test a new digital nest camera with three different activation systems.

The need to base decisions on sound scientific knowledge and determination of the identity and level of activity of nest predator species is an increasing focus of attention for Northern Lapwings. Northern Lapwing populations are continuing to decline in Wales regardless of management measures that have been implemented to try and slow or reverse this decline (see chapter two). A recent analysis of the British Trust for Ornithology's nest record card data (Chamberlain & Crick 2003) suggests that an increase in nest predation rates has contributed to Northern Lapwing population declines during the 1990s and analysis of nest predation rates in this present study reinforces the important role that predators play in determining Northern Lapwing breeding success. If any conservation initiatives are to be successful in improving Northern Lapwing breeding success then, before any predator control measures are implemented, it is imperative that predator species are correctly identified and management plans are adjusted accordingly. Therefore, the main aims of this study were i) to assess the degree of daily power consumption of each camera system, ii) to optimize image quality without increasing power consumption, and iii) to assess the effectiveness of each system in identifying Northern Lapwing nest predators.

Methods

Digital device

During 2004, a new digital device was developed and field-tested. The image storage unit was based on Video Domain Technologies Memocam DVR unit, weighing 250g and supplied in a metal enclosure that is not suitable for outdoor use. This unit has been designed for the security industry but can easily be adapted for field biological applications by mounting in an IP66 weatherproof box of 18 x 11 x 9 cm. The unit has capacity to store up to 20,000 low-resolution images on a 128Mb multi-media card (MMC). With storage capacity of the memory cards continually increasing, it is likely that the system will allow up to 80,000 images to be recorded on 512 Mb cards. Images can be downloaded using a card reader that connects directly into the USB port of a PC or laptop.

The Memocam unit is configured using Windows based software supplied with the unit. One of the many functions that are user selectable is the over-write facility when the card is full or to terminate image capture. In over-write mode, the degree of autonomy is therefore determined by power consumption rather than image storage capacity

Use was made of the Memocam Video Motion Detection (VMD) facility, to record images when activity occurred at the nest. The VMD facility allows the user to select any specific parts of the image in which motion occurs, to trigger image capture, and allows adjustment of a sensitivity setting. This can be used to great advantage, to ensure frames were stored only when relevant activity occurred. Using a low sensitivity setting and selecting only the area occupied by the nest cup ensured that images would be captured should any significant motion occur within the nest itself, but movement of vegetation surrounding the nest would not trigger image capture. The unit was configured to take three images each time the camera picture changed significantly at the nest using VMD although up to 101 images per event can be stored. The first image stored is the pre event frame and the next two subsequent ones were at 0.5 second intervals. The minimum time interval between frame storage is 0.3 seconds. A 10 second delay was then initiated between recording to reduce duplicated events. This is also software selectable from 0 to 999 seconds.

Ancillary equipment

The black and white camera used was a very low specification (240 line resolution) with 3.6mm lens supplied by Maplin (product code PH86T). It measured 22 x 14 x 14mm and to this six infra red light emitting diodes (LEDs) were attached in an array around the lens to provide night-time illumination. The LEDs (TSUS5400) had a peak wavelength of 950nm which were connected in series emitting no visible glow which can be a problem with commercial IR cameras. A basic 24 hour electronic timer (Farnell, product code 678-340) was adapted with the addition of a suitable relay to control the timing of infrared illumination. This can easily achieved using a Light Dependent Resistor or Photodiode detecting ambient light levels.

Power considerations

The Memocam image storage unit draws a current of 300mA, equating to a daily consumption of 7.2Ah. The camera and infrared illumination also require around 1Ah, which yield a total consumption of 8.2Ah per day. However, if sensors are used as triggers then the unit can be put into standby mode that reduces consumption to only 20mA, in addition to the power used by the sensor circuitry itself. Whilst the use of a standby facility can thereby greatly reduce daily power consumption, it is essential to ensure that the unit can be rapidly and reliably activated to record any predation event.

Triggering methods

Three prototypes, employing different triggering mechanisms and using a 12V 38Ah cyclic battery were trialled. On the basis of these trials the optimal trade-off between design complexity, reliability and autonomy was to be determined. These prototypes differed in their power requirements and therefore the length of autonomy before battery replacement. There is however, a trade-off between system complexity (and hence cost and probably, reliability) and autonomy. Applications with objectives other than identification of nest predators will probably require different triggering mechanisms, but are likely to present less of a technological challenge.

Option 1: Permanently active. The image capture unit was not allowed to enter stand-by mode, thus maximizing the likelihood of recording a predation event. However, this obviously results in a large number of recorded events, which take longer to

review, and requires higher daily power consumption and hence offers lower autonomy (Table 1).

Option 2: Passive Infra-red sensor. The Memocam was awoken from standby mode by the triggering of a miniature 5 metre spot passive sensor which was mounted on the camera pole just below the camera and pointing directly at the nest. Triggering (for example, by movement of the incubating bird) switched on the Memocam for the period of two minutes and activated the VMD facility. The card configuration was exactly the same as for Option 1. The major limitation of using the internal VMD is that whilst the unit is asleep the system takes 10 seconds to become ready to take images. From previous work it had been found that the adult bird generally left the nest at least one minute before the arrival of a predator. The predator would then re-trigger the system if two minutes had elapsed.

Option 3: Infra red beam. An infra-red emitter and detector were located either end of a 500mm U- shaped frame, positioned so that the beam passed directly over the nest, a few centimeters above the eggs. The frame was hidden under soil with only 50mm of the vertical frame at each end exposed in which the emitter and detector were housed. Once there was a change of state in the beam (i.e. the beam being broken or completed) the system was woken up for three minutes and the unit switched on to VMD. The Memocam was configured identically to Options 1 and 2.

Table 1. Characteristics of digital camera configurations for monitoring nest predation events

Activation system	Activation from standby mode	Image recording mechanism	Autonomy
Memocam unit permanently active	None	VMD	c. 4 days
Passive Infra-red	Motion detected by miniature NCIS 5m Spot Passive Infra-red	VMD	c. 5 days
Infra-Red beam	Light beam completed when bird leaves nest	VMD	c. 7 days

Field trials

Five camera units were field trialled at three study sites in North Wales between April and July 2004. Site 1 (Beeches Farm, 52°54'N, 2°30'W) is a 190ha mixed livestock (beef cattle and sheep) and arable farm bordering the River Dee. Site 2 (Inner Marsh Farm, 52°53'N, 2°25'W) is a 212ha arable farm with a mixture of root crops, winter wheat and long- and short-term set-aside that borders a nature reserve. Site 3 (Sealand Ranges, 52°52'N, 2°24'W) is an area of wet grassland bordering salt marsh that forms part of a Ministry of Defence firing range, and is used periodically for the grazing of large numbers of sheep. Predation was the main cause of nest failure and nest survival rates differed between the three sites with 47% of nests hatching at least one chick at site 1, 22% at site 2 and 18% at site 3.

One unit was configured according to Option 1 and two units configured according to Options 2 and 3. Northern Lapwing nests were monitored every one to two days to determine nest fate and to verify the correct functioning of the camera units.

Statistical Analyses

Generalized Linear Mixed Models in SAS version 8.2 were used to investigate daily predation rates of nests (with binomial error structure and logit link, with site and field as a random term and nest identity as a random term to control for repeated measures of nests). Analysis of daily mortality was undertaken for the period from locating the nest up to the point of hatching (at 30 days) or nest failure, with data from nests known to have failed being included up to the time of failure. Nest failure was assumed to have occurred midway between the last observation of the intact nest or incubating adult and the visit on which failure was confirmed. Clutches were defined as being in the laying stage when the clutch was found incomplete and further eggs were added, with the assumption that one egg is laid each consecutive day. Clutches were defined as being in the hatching period when cracks started to appear on the egg and chicks were heard peeping or tapping inside the egg.

In the Generalized Linear Mixed Modelling analyses described above both backwards and forwards stepwise regression was undertaken to establish model robustness and terms were added to the model at $P<0.1$ (forwards regression) and omitted from the model at $P>0.05$. Only significant terms remained in the final minimal models. Two-way interactions terms were included in the modelling procedure. Any overdispersion in the data was automatically controlled for by SAS procedures and model fit was checked by examining plots of residuals.

Other data analyses were carried out in Minitab version 12 with all dependent variables being tested for normality.

Results of field trials

Cameras were deployed on a total of 40 different nests. Due to camera and storage card failures eight nests had cameras placed next to them twice during the incubation period of that nest, and two nests had camera put in place three times throughout incubation.

Problems encountered in the field

The first major constraint of the system identified was the inability of the camera to react to high light levels during full sunlight. This prevented the VMD from working reliably as the image often appeared completely 'bleached out'. The problem was satisfactorily overcome by attaching an infra-red filter in front of the lens. The right balance between reducing high levels of sunlight was achieved with no detrimental effect to the night-time image.

A further problem encountered was the permanent corruption of the storage cards. The cause was very low battery voltage (typically below 6 V) which became evident towards the end of the season as battery life deteriorated. If the storage card was being written to as the battery voltage dropped then images on the card became corrupted and in most cases the storage card was permanently damaged, with no possibility of recovering any of the images. The addition of a low battery voltage switch off circuit after field trials resolved this problem in the laboratory.

The infra-red beam camera setup encountered the highest failure rate (number of camera failures/successful number of days recorded) of the three systems on trial with a failure rate of 0.261. In three cases, the reason for the failure was unknown. There were difficulties with correctly aligning the beam across the nest, which could explain why, in some cases, the system failed to record any images. This system also took more time to set up than the permanently active or passive infra-red systems. The passive infra-red system had the lowest failure rate (0.125 failures/successful days) and the failure rate of the permanently active system was 0.172. No ingress of liquid or condensation problems were encountered in any cameras.

A total of 10 nest failure events were recorded over the course of the season (Table 2). Three nest predation events that occurred at monitored nests were not recorded, due to a corrupted storage card in two cases, and a broken LED and poor focus in one case.

Image quality

The interrogation of digital cards was found to be very fast and key events could be located in a matter of seconds compared to long periods required to review analogue video tapes. Image quality was relatively poor at the start of the field trials (Fig.1a)

although it was still possible to identify nest predators. However, by adjusting the Memocam settings and the attaching of infra-red filters to the cameras lens image quality improved as the field trials progressed (Fig.1b).

Effect of cameras on nest survival

An analysis of daily nest predation rates revealed that the daily probability of predation varied significantly with crop type (GLMM: $F_{6,1362}$=3.19, P=0.0041), stage of incubation (GLMM: $F_{2,1362}$=43.58, P<0.0001), first egg date (GLMM: $F_{1,1362}$=11.39, P=0.0008) and distance to nearest boundary (GLMM: $F_{1,1362}$=4.04, P=0.0447). For further details and discussion of these results see chapter four. However, daily predation rates did not change significantly when cameras were present at nests (GLMM: $F_{1,1359}$=1.78, P=0.1820) and there was no evidence that cameras either increased or reduced nest predation frequencies (predation rate of nests with cameras present at some point during incubation 28/40, predation rates of nests that never had cameras 35/63; χ^2_1=0.143 P=0.143).

There was no significant difference between the number of clutches abandoned at nests with camera (n=1) and nests without cameras (n=3; χ^2_1 =0.357, P=0.550). It should be noted that given the small sample size and therefore reduced power of the analyses differences in predation frequencies or nest abandonment rates between nests with and without cameras may exist but are not being detected.

Table 2. Detection of Northern Lapwing nest predation events according to system configuration, causes of camera failure and nest predator identification.

System type	Nest days	Images recorded	Camera failures	Reason for failure	Predation events recorded	Predator identity	Predation events missed
Permanently active	23.2	54,923	4/16	Corrupt cards (3) Broken LED (1)	3	Fox (2) Badger (1)	2
Passive Infra-red	56	82,860	7/29	Corrupt cards	6	Fox (3) Badger (1) Crow (1) Sheep (1)	1
Infra-Red beam	15.3	9,263	4/7	Sheep (1) Unknown (3)	1	Fox (1)	0

Figure 1. A comparison of daytime and nighttime images recorded on cameras at the start of the field trials (a) and towards the end of the field trials (b).

1a. Daytime

1a. Nighttime

1b. Daytime

1b. Nighttime

Predator identification

Four different species were recorded taking Northern Lapwing eggs (table 3). Nine out of the ten predation events were by mammalian predators and only one avian predator was recorded. When the entire contents of the nest were taken by predators, Northern Lapwings continued to incubate for up to 123.27 (± 138.69 s.d.) minutes and only 58.4 (± 55.8 s.d.) images were recorded after the predation event. This very limited activity at the nest once the predation event had occurred meant that no key images were overwritten. However, in two cases only part of the clutch was taken by predators and the Northern Lapwings continued to incubate the remaining eggs until

hatching. Therefore, in the case of partial predation events, the possibility remains that key images identifying the predators could be overwritten.

An examination of the visible signs left by predators around the nest area did not reveal any patterns consistent to a particular predator species.

Table 3. Northern Lapwing nest predator species identification, the timing of the predation event, the time between the incubating adult leaving the nest and the predator arriving at the nest and signs left at depredated nests. * = partial predation event.

Predator species	**Time of predation event**	**Minutes between bird leaving and predator arriving**	**Types of signs left by predators at nest**	**Other species seen or leaving signs at nest**
Crow	09.15	2	no sign	none
Fox*	22.42	37	no sign	none
Fox	02.21	6	disturbed nest lining, egg yolk in scrape	none
Fox	03.58	3	no sign	none
Fox	01.44	12	egg yolk in scrape	none
Fox	23.40	6	no sign	none
Fox	00.19	0.4	no sign	none
Badger	04.13	13	hedgehog scat, fox and badger prints, yolk in scrape, eggshell ~50m from nest	fox and hedgehog
Badger	02.19	0.5	eggshell and blood in scrape, badger prints	none
Sheep*	08.49	14	egg yolk in scrape	none

Discussion

All three systems of digital camera produced images of a quality good enough to correctly identify nest predators. The addition of infra-red lenses to the cameras allowed the capture of both daytime and nighttime images without any problems occurring. The real trial however was between the three different triggering mechanisms. The permanently active system (with only the video motion detection of the Memocam software and no extra triggering mechanism) and the passive infra-red triggering system were both extremely reliable and predation events were only missed due the problem of memory card corruption. The passive infra-red system has the advantage over the permanently active system in that fewer images are recorded and therefore battery life is longer and cards have to be changed less frequently. The infra-red beam was the least reliable part of the system. The failure of this system, in some cases, to record any images was probably a result of the difficulties of correctly aligning the beam across the nest. If there was a lot of vegetation around the nest, or the nest was situated on uneven ground then it was more difficult to align the two sensors necessary for the completion of the beam. The extra wires needed for the beam sensor also meant that the system was more fragile and prone to breakage. Overall, the infra-red beam system was more time-consuming to set up and involved more disturbance around the nest than the other two systems.
In terms of depredation studies at Northern Lapwing nests, predator identification was clear and precise. Because very few images were recorded after predation events, then no predation events were recorded over. However, problems may arise when only part of the clutch is taken by a predator and the Northern Lapwing continues to incubate. In this case, it is possible that the predation event could be written over.

A comparison of visible signs left around depredated nests in order to determine predator identity was not particularly fruitful. Foxes were the main predator of Northern Lapwing nests, yet signs left by foxes were inconsistent. In two cases the eggs were eaten at the nest scrape which meant that that there were remnants of eggshells, however in four cases the entire clutch was taken leaving behind no visible signs. In soft ground mammalian footprints were visible, but as shown by the footage from one nest taken by a predator, it is possible for more than one predator species to

visit the same nest. Therefore, using footprints, or scats, may not always be a reliable indicator of the true predator identity. In the majority of cases, entire clutches were taken, by mammalian and avian predators, leaving no trace and we could find no distinct pattern of nest destruction or signs that could be used to confirm predator identity. This highlights the potential difficulties and risks of identifying some predator species by nest remains and reinforces the need for a reliable camera system which can properly identify nest predators.

This field trial has highlighted the impact that mammalian predator species can have on Northern Lapwing nest survival. The fox and crow control policy of the RSPB currently rests on an assessment of fox and crow densities and nest predation rates, on the assumption that if nest predation rates are high and fox and/or crow densities are high, then these species must be responsible for the observed nest predation. However, without reliable nest predator identification fox and/or crow control may be invoked unnecessarily in instances where other nest predators are having a big impact.

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Chapter 4.

Northern Lapwing *Vanellus vanellus* habitat selection and the impact of mammalian predators on nest survival on agricultural land

Fiona Sharpe & Mark Bolton

Abstract

This chapter examines Northern Lapwing *Vanellus vanellus* nest survival rates in the light of recent declines. Data are analysed from counts of breeding Northern Lapwings, and 286 nests found on four lowland agricultural sites in North Wales in 2003 and 2004. Northern Lapwing habitat selection and breeding densities are considered in relation to land use, and nest predation rates are modelled. Digital nest cameras are employed for the first time at Northern Lapwing nests to aid nest predator identification. Northern Lapwings showed a preference for nesting in spring crops above winter crops and grassland. The majority of recorded nest failures across all habitats were caused by predation, and the main predators identified by digital nest cameras were mammalian. Nest predation rates varied among crop types, with highest predation rates in grassland and set-aside habitats. Eggs laid later in the season were more likely to be taken by a predator than earlier nests, and nests placed closer to field boundaries were less likely to survive to hatching. Predation rates were found to be higher in nests close to hatching than during the laying period or the earlier incubation period. This suggests that predators could be using acoustic rather than visual cues to locate nests, which also implies predation by mammalian rather than avian species. Mayfield estimates indicated that only 36.6% of nests successfully hatched at least one chick which suggests that poor nest survival, caused by high predation rates, may be partly responsible for the decline of breeding Northern Lapwings on agricultural land in North Wales.

Introduction

Over recent decades birds associated with agricultural land in Britain and elsewhere in western Europe have undergone widespread declines frequently accompanied by contractions in breeding ranges (Fuller *et al.* 1995; BirdLife International 2004). These declines have been linked to agricultural intensification (Chamberlain & Fuller 2000; Chamberlain *et al.* 2000; Donald *et al.* 2001) and declines have been steeper for farmland specialists rather than generalist species (Gregory *et al.* 2004). Northern Lapwings *Vanellus vanellus* are one of the species that have been affected by recent changes in land use and land management. Between 25-49% of the global population of Northern Lapwings breed within the current 25 member states of the European Union (EU) (BirdLife International 2004), and the estimated total population for the British Isles is 205,000 – 260,000 breeding pairs (Gibbons *et al.* 1993). The EU conservation status of Northern Lapwings changed from favourable in 1994 to unfavourable in 2004. In England and Wales, the numbers of breeding Northern Lapwings have declined by 49% over an 11-year period, with the most severe decline occurring in Wales where breeding numbers fell by 77% (Wilson *et al.* 2001). Population declines may be driven by either adult or juvenile survival or by changes in breeding productivity (the number of chicks that fledge). There is no evidence to suggest that the decline in Northern Lapwings is being driven by higher adult or juvenile mortality, therefore poor breeding success up to, or just after the time of fledging, appears to be the most likely causal factor (Baines 1990; Peach *et al.* 1994; Catchpole *et al.* 1999).

Lower productivity has been linked to land use changes such as agricultural improvement of pasture, increases in livestock densities, the timing of sowing and harvesting operations, simplification of crop rotations, the regional polarisation of cereal and grassland (concentration of arable land in eastern UK and pasture in western UK) and increases in fertiliser application (Baines 1990; Chamberlain *et al.* 2001; Stephens *et al.* 2003). Such changes have been shown to affect Northern Lapwing productivity in various ways resulting in increased mortality of eggs and chicks from trampling by livestock or machinery (Beintema & Müskens 1987), direct loss of breeding habitat and declines in food availability (Wilson *et al.* 2001). Farming operations (cultivation and harrowing) after the start of breeding have been shown to

be a major cause of nest failure in cultivated landscapes (Shrubb 1990; Berg *et al.* 1992) whereas clutch predation and nest losses to trampling by livestock are more severe in grassland habitats (Galbraith 1988a; Shrubb 1990). Substantial loss of Northern Lapwing eggs to predators have been widely documented (Beintema & Müskens 1987; Galbraith 1988a; Baines 1990) and evidence has recently emerged suggesting that more recent Northern Lapwing population declines could be influenced by increased clutch failure rates mediated by increased grazing pressure in marginal uplands and increased nest predation rates across all habitats (Chamberlain & Crick 2003). Predators of Northern Lapwing eggs include Carrion Crows *Corvus corvus corone*, Magpies *Pica pica*, foxes *Vulpes vulpes*, badgers *Meles meles*, hedgehogs *Erinaceus europaeus* and mustelids *Mustelidae* (Trolliet 2003) and there is evidence that eggs tend to be more vulnerable to predation during the laying stage than during incubation (Beintema & Müskens 1987). Although the main nest predators have been identified, the relative impact of predator species is still unknown and it is unclear whether the influence of different predator species alter under different circumstances, for example according to habitat or availability of alternative prey. Although Northern Lapwings, as ground nesting birds, are susceptible to high nest losses, they do have the ability to compensate for this by relaying replacement clutches and are capable of laying up to five clutches in one season (Klomp 1951). However, despite this ability to compensate for nest losses, nest failures rates have risen sharply since the 1980's (Chamberlain & Crick 2003) possibly contributing to recent population declines.

In assessing the importance of any habitat to breeding birds, it is necessary to determine not only breeding densities supported but also the contribution made to overall recruitment in terms of the number of chicks that successfully fledge on that habitat. In general, Northern Lapwings prefer to nest on arable land rather than pasture and spring-sown crops are the preferred crop (Galbraith 1988a; Berg *et al.* 2002). When the chicks hatch they tend to move into pasture and grassland to find suitable foraging areas (Hudson *et al.* 1994) and consequently Northern Lapwings prefer to nest in arable fields adjacent to pasture (Galbraith 1998a). However, Northern Lapwings do not always show a preference for breeding on arable land (see Blomqvist & Johannson 1995), especially in areas where agriculture is not yet intensive.

Northern Lapwings usually breed in semi-colonial aggregations. Colony size has been shown to have a positive effect on reducing avian nest predation rates (Elliot 1985; Berg *et al.* 1992) and the risk of nest predation is higher for solitary nests (Seymour *et al.* 2003). Nest site choice and nest predation rates have also been shown to be influenced by the presence and distance from potential predator perches (Berg *et al.* 1992), roads (Van der Zande *et al.* 1980) and electricity pylons (Milsom *et al.* 2000).

This study examines environmental factors related to variation in Northern Lapwing habitat selection and nest survival rates at four study areas in North Wales. Nest survival is investigated in relation to crop type, field characteristics, distance to nearest neighbour and colony size as well as seasonal variations. In particular we examine predation risk in relation to incubation stage, and the importance of predation as a cause of nest failure and identify the main predators through the use of digital nest cameras. Nest survival rates are compared to those reported in previous studies and the causes and the role of nest mortality in relation to the decline of Northern Lapwing breeding around the Dee Estuary, North Wales are considered.

Study areas

Research was undertaken across four study sites in Flintshire, North Wales in 2003 and 2004. Study sites were located on the low-lying ground in the vicinity of the River Dee. The main land-uses in this area were the growing of arable crops, especially potatoes, onions, leeks, maize and winter cereal with smaller areas of rough and improved grassland. The population of breeding Northern Lapwings around the Dee Estuary in 2002 was estimated at approximately 300 pairs (C. Wells, unpublished data), and the four study sites held approximately one third of the Dee population. Site 1 (Beeches Farm, 52°54′N, 2°30′W) is a 190ha mixed livestock (beef cattle and sheep) and arable farm bordering the River Dee. In 2003 this farm joined an agri-environment scheme (Tir Gofal) incorporating Northern Lapwing prescriptions that included marking and avoiding nests. Site 2 (Inner Marsh Farm, 52°53′N, 2°25′W) is a 212ha arable farm with a mixture of root crops, winter wheat and long- and short-term set-aside that borders a nature reserve. Site 3 (Sealand Manor 52°44′N, 2°27′W) is a 130ha area of intensively farmed arable land consisting mainly of winter wheat,

potato and onion crops. Site 4 (Sealand Ranges, 52°52'N, 2°24'W) is an area of wet grassland bordering salt marsh that forms part of a Ministry of Defence firing range, and is used periodically for the grazing of large numbers of sheep.

A wide range of potential predators were present on all study sites including Carrion Crows, Magpies, Ravens *Corvus corax*, foxes, mustelids and badgers.

Methods

Nest characteristics and surveys

Nests were located by observing incubating adults from a hide or car, or by walking transects of fields. The length and maximum breadth of each egg was measured to the nearest 0.1mm using callipers, and the position of each nest was recorded using a Garmin Etrex© handheld GPS recorder. Each egg was floated in lukewarm water to establish an expected date of hatching (based on a chart developed by O. Pineau for the Kentish Plover *Charadrius alexandrinus*), and to estimate the laying date of the clutch (the date the first egg in the clutch was laid based on a 30-day laying and incubation period). Egg volume (cm^3) was calculated as length × $breadth^2$ × 0.457 (Galbraith 1988b). A weekly census of each study site was carried out. Data were collected on a field-by-field basis by either scanning the entire field from a car or a vantage point. The locations of Northern Lapwings in each field were recorded onto maps. The population size was determined as the maximum count between 15th April and 31st May divided by two (Barrett & Barrett 1984, O'Brien & Smith 1992). The behaviour of Northern Lapwings was also recorded to aid nest location. A record of the crop type in each field and whether any farming operations had taken place since the previous visit was also made. The availability of different habitats was mapped and the area calculated using 1:25,000 maps. The size of the colony that each nest belonged to was determined as the number of active nests within a 200m radius.

Nests were checked regularly (every 4 - 8 days). If a parent was seen incubating then the nest was assumed to be active. If no bird was seen incubating then the nest was visited to check that the contents were intact. Nests were recorded as successful if at least one hatched chick was seen, or if the nest was due to hatch and either small fragments of egg shell were found in the bottom of the nest scrape or the behaviour of

adults around the nesting area indicated successful hatching. Nests were recorded as being taken by a predator if they were empty before the expected the hatch date and no signs of chicks were seen, or if there was direct evidence of predation (i.e. large egg shell fragments or yolk in the scrape, disturbed nest lining etc.). When no parent was seen incubating and the eggs felt cold to touch one egg was placed with the pointed end facing outwards and if it was still in the same position then following day, the nest was recorded as abandoned. Nest destruction by farming practices was identified when the whole clutch disappeared in conjunction with machinery operations taking place in the field.

Digital nest cameras, where movement at the nest triggered image capture, were used to record predation events at 10 nests (see Chapter 3).

Statistical analyses

Nesting habitat preferences were examined using Jacob's Selectivity Index ranging from –1 (total avoidance of a particular habitat) to +1 (total preference for a particular habitat). Jacob's Selectivity Index (D) was calculated as $D = (r-p)/(r+p-2rp)$, where r = the proportion of birds in the area of interest compared to the proportion of birds in the whole study area and p = the proportion of the field area of interest compared to the total field area of study.

Generalized Linear Mixed Models in SAS version 8.2 were used to investigate (i) variation in the number of breeding pairs of Northern Lapwing per hectare (with normal error structure and identity link, with field and site as random terms); (ii) variation in clutch size (the probability of laying a four egg clutch: with binomial error structure and logit link, with field and site as random terms to control for non-independence of nests within the same field and study sites); (iii) daily predation rates of nests (Aebischer 1999) with binomial error structure and logit link, with site and field as random terms and nest identity as a random term to control for repeated measures of nests). Analysis of daily mortality was undertaken for the period from locating the nest up to the point of hatching (at 30 days) or nest failure, with data from nests known to have failed being included up to the time of failure. Nest failure was assumed to have occurred midway between the last observation of the intact nest or incubating adult and the visit on which failure was confirmed. Clutches were defined

as being in the laying stage when the clutch was found incomplete and further eggs were added, with the assumption that the laying interval between successive eggs was two days (Galbraith 1988a). Clutches were defined as being in the hatching period when cracks started to appear on the egg and chicks were heard calling or tapping inside the egg.

In the Generalized Linear Mixed Modelling analyses described above both backwards and forwards stepwise regression was undertaken to establish model robustness and terms were added to the model at $P < 0.1$ (forwards regression) and omitted from the model at $P > 0.05$. Only significant terms remained in the final minimal models. Two-way interactions terms were included in the modelling procedure. Any overdispersion in the data was automatically controlled for by SAS procedures and model fit was checked by examining plots of residuals. Other analyses were carried out in Minitab version 12 with all dependent variables being tested for normality.

Results

Habitat selection and nesting densities

Over the course of the breeding season, Northern Lapwings' preferences for nesting in different crop types changed (Table 1). Overall Northern Lapwings exhibited a strong avoidance of winter cereal throughout the breeding season and they exhibited a strong preference for nesting in maize and spring cereal crops habitat. Towards the end of the breeding season Northern Lapwings started to avoid nesting in spring cereal, tillage, rough grazing and potato and onions crops, and overall they showed no preference or avoidance of rough grazing, set-aside, tillage or potatoes and onions.

Higher densities of breeding pairs were found in fields adjacent to pasture/wet grassland (0.66 pairs ha^{-1} ± 0.06 se) than in fields not adjacent to pasture/wet grassland (0.26 pairs ha^{-1} ± 0.10 se; GLMM: $F_{1,31} = 7.91$, $P = 0.008$). There was a difference in breeding densities of Northern Lapwings between different crop types (GLMM: $F_{5,32} = 2.57$, $P = 0.046$). Breeding Northern Lapwings occurred at the

highest densities in spring cereal crops and the lowest densities in winter cereal (Fig. 1).

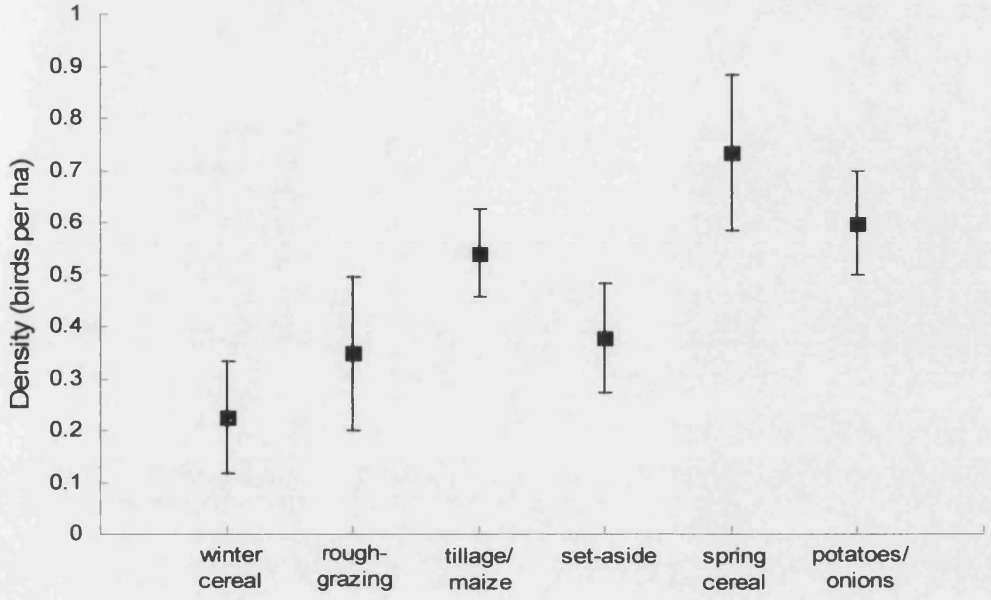

Figure 1. The breeding density of Northern Lapwings in different crop types (means ± 1 se).

We found no relationship between breeding densities and field size (GLMM: $F_{1,23}$ = 0.34, P = 0.567), presence or absence of pylons (GLMM: $F_{1,27}$ = 0.09, P = 0.771), distance to nearest road (GLMM: $F_{1,26}$ = 0.19, P = 0.664) or year (GLMM: $F_{1,21}$ = 0.40, P = 0.536). See appendix for details of full and final model (page i).

Clutch characteristics and causes of nest failure

Clutches were laid between 21st March and 30th May. The average clutch size was 3.80 ± 0.53 sd eggs. There was no trend for a seasonal decline in the number of eggs laid in each clutch (GLMM: $F_{1,227}$ = 1.85, P = 0.175), and there was no significant variation in clutch size according to crop type (GLMM: $F_{6,222}$ = 1.02, P = 0.414) or year (GLMM: $F_{1,227}$ = 2.36, P = 0.126).

The percentage of nests surviving from laying to hatching assuming a 30 day incubation period that included egg-laying was 36.6% (Mayfield estimate). Of the 286 nests followed until hatching or failure, 106 (37.1%) of nests successfully hatched one or more chicks, 135 (47.2%) were lost to predators and 45 (15.7%) failed due to other

causes. Other causes of nest failure included destruction of nests by farming operations (n = 23 nests, 12.8% of all failures), abandonment (n = 12, 6.7% of all nest failures) and unknown (unable to determine if nests were trampled or depredated, n = 10, 5.5% of all nest failures).

Amongst successful clutches there were 98 nests of known clutch size. In 74.5% of cases (n = 73) all eggs hatched, in 19.4% of nests (n = 19) one egg failed to hatch, two eggs failed to hatch in four nests (4.1% of nests) and three eggs failed to hatch in two nests (2% of nests). The mean number of eggs hatching at successful nests was 3.54 ± 0.74 sd.

There was no difference in the hatching rates (the proportion of eggs that hatched in successful nests) between different crop types (One-way ANOVA, $F_{6,92} = 0.217$, $P = 0.942$), and there was no correlation between hatching rates and the timing of laying ($R^2 = 0.001$, $F_{1,97} = 0.052$, $P = 0.819$).

Northern Lapwing nest predators

The major cause of nest failure was predation and in most cases the identity of nest predators was not known. However, 10 predation events were recorded by digital nest cameras. In six instances the predator was a fox, two were badgers, one a crow and one a sheep. In the case of the sheep and one fox predation event, only part of the full clutch was taken and the parent(s) continued to incubate the remaining eggs. In all other cases the entire clutch was taken.

Digital nest cameras were not placed at all sites or in all crop types, however the predation events captured give an indication of the types of predators that take Northern Lapwing nests.

Nest survival

The overall mean daily survival rate (all crop types and years combined) was 0.967 and the overall mean daily predation rate (all crop types and years combined) was 0.027. There was a significant positive relationship between daily nest predation rates and laying date (GLMM: $F_{1,3022} = 6.42$, $P = 0.0113$) and a negative relationship between daily nest predation rates and distance from the nest to the nearest field

boundary (GLMM: $F_{1,3022} = 6.03$, $P = 0.0142$). Daily predation rates were highest during the three days prior to hatching (Fig. 2, GLMM: $F_{2,3022} = 84.67$, $P < 0.0001$).

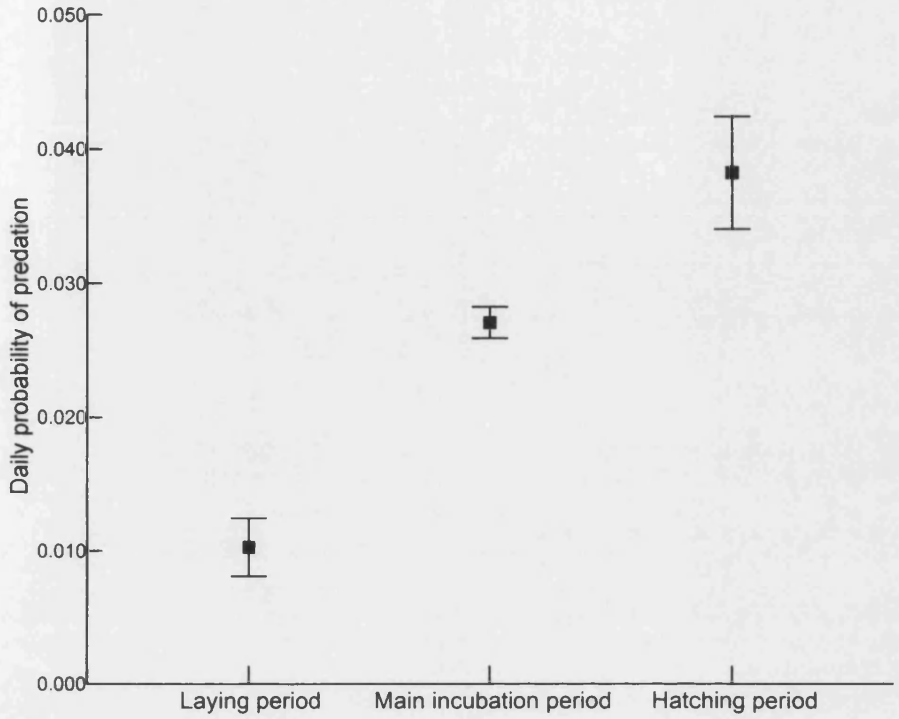

Figure 2. The mean (± 1 se) daily predation rates (probability of predation) of nests during the egg laying period, the main incubation period and the hatching period. See appendix (page ii) for results of post hoc pairwise comparison.

Table 1. Jacob's Selectivity Indices for Northern Lapwing nesting preference across all available crop types over the course of the breeding season. Indices below –0.25 (in italics) indicate avoidance and indices above 0.25 (in bold) indicate a preference. -1 = total avoidance of available habitat, +1 = total preference for nesting in available habitat.

	Breeding season							
Habitat	*Mar 14-31*	*Apr 1-14*	*Apr 15-30*	*May 1-14*	*May 15-31*	*June 1-14*	*June 15-end*	*Mean preference*
Winter wheat	**0.34**	-0.08	*-0.50*	*-0.68*	*-0.81*	*-1*	*-1*	*-0.53*
Rough grazing	0.18	0.05	0.14	*-0.25*	-0.02	*-0.41*	*-0.48*	-0.11
Maize	-	-	**0.40**	**0.48**	**0.66**	**0.70**	**0.35**	**0.52**
Set-aside	0.14	0.15	0.10	0.13	-0.05	*-0.25*	-0.06	0.02
Tillage	-0.15	0.03	0.1	**0.26**	*-0.40*	*-0.75*	*-0.62*	-0.22
Spring cereal	-	-	**0.97**	**0.97**	**0.86**	-0.15	*-0.28*	**0.47**
Potatoes/ onions	0.12	**0.30**	0.19	-0.02	*-0.30*	*-0.36*	*-0.97*	-0.15
Mean Northern Lapwing count	229	221	219	190	145	112	76	

Daily nest predation rates for nests in rough grazing and set-aside were almost twice as high as other crop types and these figures correspond to only 12% of nests hatching in rough grazing, 15% in set-aside, 40% in winter cereal, 44% in tillage, 52% in maize, 61% in spring cereal and 70% in potatoes and onions (Fig. 3, GLMM: $F_{6,3022} = 2.47$, $P = 0.0218$).

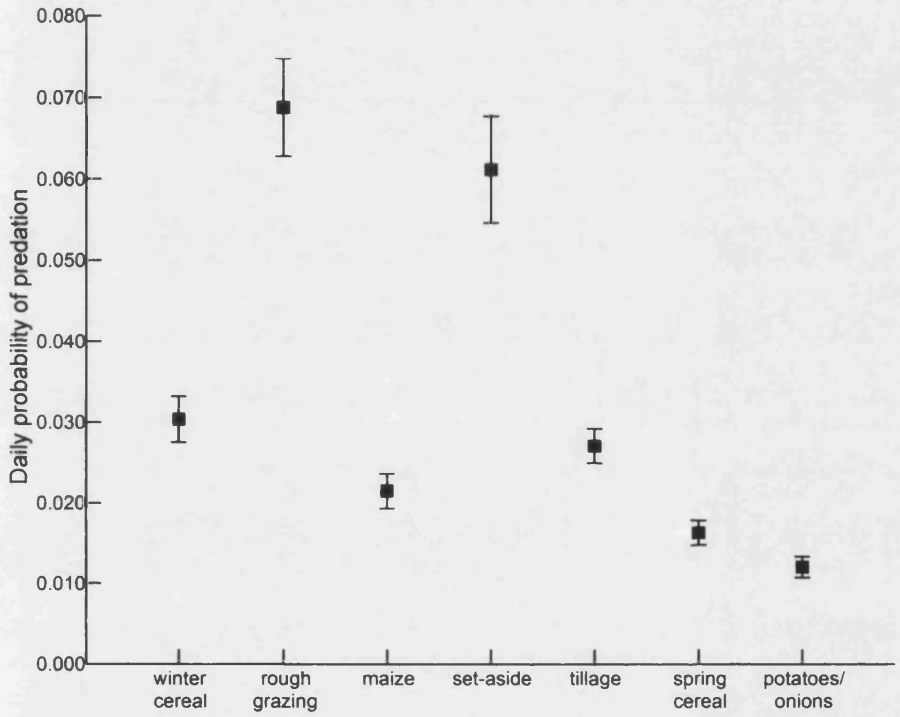

Figure 3. The mean (± 1 se) daily predation rates (probability of predation) of nests in different crop types (both years combined). See appendix (page ii) for results of post hoc pairwise comparison.

There was no significant relationship between daily nest failure rates and colony size (GLMM: $F_{1,3028} = 1.06$, $P = 0.3036$), distance to nearest predator perch (GLMM: $F_{1,3027} = 0.49$, $P = 0.4840$), distance to nearest neighbour (GLMM: $F_{1,3028} = 0.16$, $P = 0.6922$) or year (GLMM: $F_{1,3027} = 0.53$, $P = 0.4655$). See appendix (page i) for details of full and final model.

Discussion

Although well over half of all nests failed to survive to hatching, nesting success fell within the range of that recorded in previous studies (Galbraith 1988a: arable 28.2%, rough grazing 34.3%; Trolliet 2003: 35.4 – 76%), yet it was substantially below the average of 58.4% (Trolliet 2003). A review of the breeding productivity estimates from a number of studies across Europe showed that only five out of 14 populations attained the required levels of productivity to maintain stable breeding populations (Hudson *et al.* 1994) suggesting that many nest survival estimates are based on declining populations. The number of nests destroyed directly by farming operations was minimal across all habitats and predation rather than agricultural operations was the main determinant of nest failure.

Spring cereals were one of the preferred nesting habitats for Northern Lapwings, and Northern Lapwing nest survival was also high in these crops. However, spring cereals accounted for less than 2% of the available habitat and the number of nests that were laid on spring cereal only accounted a small proportion of the total nests found. A relatively large proportion of nests were found in tilled fields and fields planted with maize and potatoes or onions. Predation rates in these habitats were also relatively low especially in comparison to the high predation rates in rough grazing and set-aside. Northern Lapwings show a preference for nest sites with short or no vegetation (Galbraith 1988a; Berg *et al.* 1992), for example, bare tilled land or on bare patches within sprouting arable crops (Shrubb 1990) and particularly those fields in the proximity to suitable feeding fields for adults and chicks (Galbraith 1989). This preference is primarily due to the existence of good feeding conditions for breeding females, camouflaged concealment of unattended nests, and clearer views of any approaching predators (Hudson *et al.* 1994). Nest predation rates may be linked to vegetation height. Sward height is known to influence Northern Lapwing nest site choice with birds leaving or avoiding fields when the sward becomes too dense and tall (Lister 1964; Shrubb & Lack 1991). Increased fertiliser applications to achieve higher crop yields, and the switch from spring-sown to autumn-sown crops have led to increased growth and uniformity of vegetation during the breeding season (Hudson *et al.* 1994; Vickery *et al.* 2001). As sward height increases throughout the breeding

season, the ability of incubating Northern Lapwings to detect approaching predators diminishes (Vickery *et al.* 2001).

Northern Lapwing nest predation rates have also been shown to be influenced by the distance to linear features such as field boundaries and roads, or predator perches (Van der Zande *et al.* 1980; Berg *et al.* 1992; Milsom *et al.* 2000; Sheldon 2002). Field boundaries may act as dispersal corridors for foxes and other predators and foxes have been recorded as systematically searching for prey along the edges of dykes and shallow ditches (Seymour *et al.* 2004; personal observation). Many field boundaries also consisted of hedges or fences which could be potential perches for avian predators. However, the absence of a relationship between nest survival and distance to the nearest predator perch could either be because potential predator perches were incorrectly identified or avian predators (especially corvids which are known to use perches whilst searching for nests) were not responsible for many nest failures.

Evidence gathered from digital nest cameras indicated that foxes were the main predators of Northern Lapwing nests in this study. A study of the predation behaviour of foxes around Northern Lapwing nests has previously suggested that that nest losses to foxes are expected to be incidental (Seymour *et al.* 2003). Several studies have provided evidence for the importance of avian predators, particularly Carrion Crows, as predators of Northern Lapwing nests (Baines 1990; Berg *et al.* 1992). In comparison, foxes are seen as relatively inefficient Northern Lapwing nest predators (Seymour *et al.* 2003). However, evidence from this study suggests that fox predation may be more important in Northern Lapwing populations than previously shown. The tendency of Northern Lapwings to breed in colonies and to display aggressive anti-predator behaviour has been shown to reduce predation by corvids (Göransson *et al.* 1975; Elliot 1985; Berg 1996), yet Northern Lapwing anti-predator behaviour appears to be largely ineffective against large mammalian predators such as foxes and badgers (personal observation), therefore, the absence of a correlation between colony size or distance to nearest neighbour and nest survival may be a consequence of foxes and badgers being largely responsible for the majority of nest predations.

Nest survival rates have been shown to be lower in the laying period than during the incubation period in Curlews *Numenius arquata* (Grant *et al.* 1999) and Northern Lapwings (Beintema & Müskens 1987) which is in contrast to the findings of this study. The study on Curlews suggested that higher failure rates during the laying stage were due to a greater vulnerability of nests to predators and both avian predators and foxes were identified as being important in determining nest survival rates. However the daily predation rate appears to be higher during the laying period on sites where the main predators were avian, and foxes were generally absent (Grant *et al.* 1999). This raises the question as to what cues different predators use to locate the nests of ground-nesting birds. Crows are well-known for using perches from which to observe and determine the location of nests whereas nocturnal predators such as badgers and foxes locate prey by acoustic and olfactory cues. It is likely that some, if not most, fox predations are incidental as suggested by Seymour *et al.* (2003). However, experimental studies involving captive foxes showed that acoustic cues were particularly important in stimulating and directing search behaviour (Österholm 1964). Therefore, it is possible that the increased predation rates during the hatching stage be explained by mammalian predators stimulated into searching for nests by acoustic cues, for example chicks calling and tapping from inside the eggs. It is worth noting that when searching for nests in the process of hatching and newly hatched chicks, it was possible in many cases to locate the nest or chick through continued calling by the chicks despite warning calls of the adults.

Northern Lapwings are continuing to decline across the EU and the rest of Europe. As the EU continues to expand and more countries come under the influence of the European Common Agricultural Policy (the main cause of farming intensification) it is likely that Northern Lapwings will become increasingly dependent on intensively cultivated land. This study highlights the poor nest survival rates and the importance of predators in determining the survival of Northern Lapwing nests on agricultural land. In particular, there is evidence from digital nest cameras and the high predation rates during the hatching stage that mammals are responsible for the majority of nest losses. Advances in digital technology and development of reliable, cost effective miniature cameras for remote monitoring offers a valuable prospect of obtaining large visualised datasets on the predation rates of individual predator species.

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Appendix

Lapwing breeding densities

Full model:

Effect	D.F.	F statistic	P-value
Habitat	5,26	2.77	0.0479
Adjacent grass	1,24	4.29	0.0490
Year	1,21	0.09	0.7670
Distance to road	1,20	0.01	0.9412
Pylon presence	1,20	0.19	0.6679
Field size	1,19	0.00	0.9869

Minimal model:

Effect	D.F.	F statistic	P-value
Habitat	5,32	2.57	0.046
Adjacent grass	1,31	7.91	0.008
Terms dropped			
Year	1,21	0.40	0.536
Distance to road	1,26	0.19	0.664
Pylon presence	1,27	0.09	0.771
Field size	1,23	0.34	0.567

Nest survival

Full model:

Effect	D.F.	F statistic	P-value
Habitat	6,3003	0.02	0.9988
Lay date	1,3003	5.88	0.0154
Incubation period	2,3003	0.03	0.9988
Distance to field boundary	1,3003	15.22	<0.0001
Colony size	1,3003	0.58	0.4451
Distance to predator perch	1,3003	9.26	0.0024
Distance to neighbour	1,3003	0.71	0.3982
Year	1,3003	3.69	0.0548
Habitat*Incubation period	11,3003	0.39	0.9998
Lay date*Incubation period	2,3003	0.87	0.4180

Minimal model:

Effect	D.F.	F statistic	P-value
Habitat	6,3022	2.47	0.0218
Lay date	1,3022	6.42	0.0113
Incubation period	2,3022	84.67	<0.0001
Distance to field boundary	1,3022	6.03	0.0142
Terms dropped			
Colony size	1,3028	1.06	0.3036
Distance to predator perch	1,3027	0.49	0.4840
Distance to neighbour	1,3028	0.16	0.6922
Year	1,3027	0.53	0.4655
Habitat*Incubation period	6,3018	2.06	0.0546
Incubation period*Lay date	1,3025	1.08	0.2988

Post hoc pairwise comparison of clutch predation rates among different crop types

Differences of Least Squares Means

Effect	hab	hab	Estimate	Standard Error	DF	t Value	Pr > |t|
hab	1	2	-2.3463	1.6382	3022	-1.43	0.1522
hab	1	4	0.6646	1.3592	3022	0.49	0.6249
hab	1	5	-1.1854	1.0017	3022	-1.18	0.2367
hab	1	6	0.6654	1.1269	3022	0.59	0.5549
hab	1	7	1.1718	1.2804	3022	0.92	0.3602
hab	1	10	1.6965	1.0302	3022	1.65	0.0997
hab	2	4	3.0109	1.5214	3022	1.98	0.0479
hab	2	5	1.1609	1.5077	3022	0.77	0.4414
hab	2	6	3.0117	1.4474	3022	2.08	0.0375
hab	2	7	3.5181	1.5564	3022	2.26	0.0239
hab	2	10	4.0428	1.4731	3022	2.74	0.0061
hab	4	5	-1.8500	1.1404	3022	-1.62	0.1049
hab	4	6	0.000858	0.7376	3022	0.00	0.9991
hab	4	7	0.5072	0.9860	3022	0.51	0.6070
hab	4	10	1.0319	1.0860	3022	0.95	0.3421
hab	5	6	1.8508	0.9329	3022	1.98	0.0473
hab	5	7	2.3572	1.0963	3022	2.15	0.0316
hab	5	10	2.8819	0.9104	3022	3.17	0.0016
hab	6	7	0.5063	0.7408	3022	0.68	0.4943
hab	6	10	1.0311	0.9403	3022	1.10	0.2730
hab	7	10	0.5247	1.1125	3022	0.47	0.6372

Habitat codes: hab 1=winter cereal, hab 2=rough grazing, hab 4=maize, hab 5=set-aside, hab 6=tillage, hab 7=spring cereal, hab 10=potatoes/onions.

Post hoc pairwise comparison of clutch predation rates during the egg laying stage, the main incubation stage and the hatching period

Differences of Least Squares Means

Effect	incperiod	incperiod	Estimate	Standard Error	DF	t Value	Pr > |t|
incperiod	1	2	-4.3025	0.7108	3022	-6.05	<.0001
incperiod	1	3	-7.3097	0.7527	3022	-9.71	<.0001
incperiod	2	3	-3.0072	0.2564	3022	-11.73	<.0001

Incubation period codes: incperiod 1=egg laying stage, incperiod 2=main incubation stage, incperiod 3=hatching period.

Chapter 5.

Proximate and ultimate causes of high chick mortality in Northern Lapwing *Vanellus vanellus* on agricultural land

Fiona Sharpe, Mark Bolton & Tamás Székely

Abstract

Many wader species, including the Northern Lapwing, are declining throughout Europe including the UK. Poor breeding success up to, or just after the time of fledging, has been suggested as the most likely contributory factor to these declines. Studies were undertaken in 2003 and 2004 across four mainly arable sites around the Dee Estuary in North Wales. We investigated Northern Lapwing chick growth, body condition and survival in relation to crop type, crow densities, clutch characteristics and weather. Chick body condition during development was related to crop type and egg volume, and egg volume, in turn, was related to the timing of egg-laying. The growth rate of chicks across the four breeding sites was slower than growth rates reported in previous studies. Body condition relative to previous studies was poor suggesting chicks were unable to find sufficient food to sustain healthy growth. Daily chick survival rates indicated that less than 1% of chicks would have survived the 35 days from hatching to fledging. This value is extremely low, and substantially less than reported by seven previous studies. Productivity was insufficient to maintain a stable breeding population of Northern Lapwings in the study area. Predation was the main proximate cause of chick failure accounting for 90.4% of mortality of 52 radio-tagged chicks. A further 7.7% of radio-tagged chicks died from other causes (starvation or unknown), and only one chick survived beyond the battery life of the tag (21 days). Whilst high predation rates of chicks could be viewed as evidence for a causal relationship between predation and the observed low Northern Lapwing productivity, there was evidence that chicks were in poor body condition, presumably due to inadequate availability of invertebrate food: the majority of chicks that escaped predation then died of starvation. Thus management to improve food availability for chicks may be just as important as predator control to improve Northern Lapwing productivity. Further work to examine food availability is required. The impact of different predator species on Northern Lapwing chick survival needs to be further elucidated in order to implement successful conservation strategies in future.

Introduction

Several wader species, such as the Northern Lapwing *Vanellus vanellus*, Eurasian Curlew *Numenius arquata*, Common Redshank *Tringa totanus* and Common Snipe *Gallinago gallinago* are undergoing widespread declines in abundance and range across Europe (O'Brien & Smith 1992; Henderson *et al.* 2002; BirdLife International 2004; Wilson *et al.* 2005). Many of these declines have been attributed to changes in agricultural practices. Changes in management of farmland that have been implicated in wader population declines include the agricultural improvement of pasture, increases in livestock densities, the timing of sowing and harvesting operations, simplification of crop rotations, the polarisation of cereal and grassland (for example the concentration of arable land in eastern UK and pasture in western UK), and increases in fertiliser application (Baines 1990; Chamberlain *et al.* 2001; Stephens *et al.* 2003). Such land-use changes have resulted in increased mortality of eggs and chicks from trampling by livestock or machinery (Beintema & Müskens 1987; Berg 1992), direct loss of breeding habitat and declines in food availability (Green 1988; Wilson *et al.* 2001). The subsequent impacts on wader breeding success have been widely documented, and conservation initiatives have been implemented with the intention of increasing productivity through habitat management.

However, there is increasing evidence that other factors may also be important in causing declines in wader populations. In many bird species, predation is the major cause of egg and chick losses (Ricklefs 1969; Newton 1988), particularly predation by generalist predators such as corvids and foxes *Vulpes vulpes* (Tapper 1992; Gregory & Marchant 1996). In wader populations substantial loss of eggs and chicks to predators has been widely documented (Beintema & Müskens 1987; Galbraith 1988a; Baines 1990; Berg 1992; Grant *et al.* 1999), but only a few studies have found predation rates high enough be a possible cause of population decline (Parr 1992, 1993; Grant *et al.* 1999). Little is still known about the identity of many predator species especially predators responsible for chick losses, or the impact of predation on wader population trends.

Over the past few decades the numbers of breeding Northern Lapwing in the UK have declined dramatically (Baillie *et al.* 2005). Between 1987 and 1998 there was a 49%

decline in Northern Lapwing across England and Wales, with the most severe decline occurring in Wales where numbers fell by 77% (Wilson *et al.* 2001). Poor breeding success up to, or just after the time of fledging, has been the most likely contributory factor in this (Baines 1990; Peach *et al.* 1994; Catchpole *et al.* 1999), and the decline would have been more marked if not for the fact that there was a 13% increase in average adult life expectancy between 1963 to 1990 (Catchpole *et al.* 1999). The causes of nest failure have been widely studied (Shrubb 1990; Chamberlain & Crick 2003; see review Trolliet 2003) and are relatively easy to determine. However, although Northern Lapwings are susceptible to nest losses from a wide variety of sources, they are also able to compensate for these losses by relaying replacement clutches and are capable of laying up to five clutches in one season (Klomp 1951). In view of the ability of Northern Lapwings to lay replacement clutches, it is likely that chick mortality, rather than egg losses, is the main determinant of low productivity in many Northern Lapwing populations (Hudson *et al.* 1994; Trolliet 2003).

The main causes of chick mortality are adverse weather conditions, food shortage and predation, all of which are more or less interrelated (Trolliet 2003). Chick survival may have declined due to food shortage, either due to increased application rates and efficacy of pesticides, or due to losses of food-rich habitats such as pasture within arable landscapes. Chicks are also vulnerable to predation when moving between natal habitats and foraging areas (Galbraith 1988a). The polarisation of farming systems and the subsequent loss of mixed farming as well as changes in cropping types and changes in sward structure may have increased predation risk to chicks. McNamara & Houston (1987) suggested that it is inappropriate to argue that either food alone or predation alone can limit the size of a population, and that these factors cannot be considered in isolation. Individuals can decrease the probability of starvation by allocating more time to foraging behaviour, or by feeding in more risky locations but in doing so expose themselves to higher predation risk (Cuthill & Houston 1997). Therefore, a decrease in food availability may not manifest itself in an increase in the percentage of animals that starve (McNamara & Houston 1987).

It is expected that chicks in better condition have a greater probability of surviving until fledging, whereas chicks in poor condition are at a higher risk of starvation. Various factors have been found to influence Northern Lapwing chick growth and

condition including crop growth (Galbraith 1988b; Hudson *et al.* 1994), weather conditions (Beintema & Visser 1989a) and egg volume (Galbraith 1988c). In addition, Galbraith (1988c) found that the survival of chicks up to ten days after hatching was positively influenced by egg size. However, similar work carried out by Blomqvist *et al.* (1997) suggested that although egg size did affect chick survival, the effect was not independent of parental quality. Galbraith (1988c) also found that egg size on arable land was smaller in two egg clutches than three or four egg clutches, although clutches of two eggs comprised less than 5% of all arable clutches.

In this study the body condition and survival rates of Northern Lapwing chicks were measured in four study areas in North Wales. Body condition and survival were investigated in relation to crop type, weather, clutch size, egg volume and Carrion Crow *Corvus corone corone* densities, as well as seasonal variations. The importance of predation as a cause of chick failure is assessed for all areas. Estimates of fledging success are compared to those reported in previous studies, and the role of predation in the decline of Northern Lapwing breeding around the Dee Estuary, North Wales is considered.

Methods

Study areas

Research was undertaken across four study sites in Flintshire, North Wales between March – August in 2003 and 2004. Study sites were located on the low-lying ground in the vicinity of the River Dee. The main land-uses in this area were arable crops, especially potatoes, onions, leeks, maize and winter cereal with smaller areas of rough and improved grassland. The population of breeding Northern Lapwings around the Dee Estuary in 2002 was estimated at approximately 300 pairs (C. Wells RSPB, unpublished data), and the four study sites held approximately one third of the Dee population. Site 1 (Beeches Farm, 52°54′N, 2°30′W) is a 190ha mixed livestock (beef cattle and sheep) and arable farm bordering the River Dee. In 2003 this farm joined an agri-environment scheme (Tir Gofal) incorporating Northern Lapwing prescriptions. Site 2 (Inner Marsh Farm, 52°53′N, 2°25′W) is a 212ha arable farm with a mixture of

root crops, winter wheat and long- and short-term set-aside which borders a nature reserve. Site 3 (Sealand Manor 52°44'N, 2°27'W) is a 130ha area of intensively farmed arable land consisting mainly of winter wheat, potato and onion crops. Site 4 (Sealand Ranges, 52°52'N, 2°24'W) is an area of wet grassland bordering salt marsh that forms part of a Ministry of Defence firing range, and is used periodically for the grazing of large numbers of sheep.

A wide range of potential predators were present on all study sites including Carrion Crow, Common Magpie *Pica pica*, Common Raven *Corvus corax*, fox, mustelids and badger *Meles meles* as well as various raptors (Common Buzzard *Buteo buteo*, Eurasian Sparrowhawk *Accipiter nisus*, Common Kestrel *Falco tinnunculus*). Predator control measures were undertaken on Site 1 (controlling of crow and fox numbers) and Site 3 (controlling of fox numbers).

Nest characteristics and surveys

Nests were located by observing incubating adults from a hide or car, or by flushing incubating adults by walking transects of fields. 150 nests were located in 2003 and 135 nests were located in 2004. The length and maximum breadth of each egg was measured to the nearest 0.1mm using callipers and the position of each nest was recorded using a Garmin Etrex© handheld GPS recorder. Each egg was floated in lukewarm water to establish an expected date of hatching (based on a chart developed by O. Pineau for the Kentish Plover *Charadrius alexandrinus*), and to estimate the laying date of the clutch (the date the first egg in the clutch was laid based on a 30-day laying and incubation period). Egg volume (cm^3) was calculated as length × $breadth^2$ × 0.457 (Galbraith 1988c). A weekly census of Northern Lapwing on each study site was carried out. Data were collected on a field by field basis by either scanning the entire field from a car or a vantage point. The locations of Northern Lapwings and crows in each field were recorded onto maps. The behaviour of Northern Lapwings was also recorded to aid nest location and to determine the presence of chicks. Crow density was calculated as the number of crows recorded during each weekly census divided by the site area (ha). A record of the crop type in each field and whether any farming operations had taken place since the previous visit was also made.

An independent survey of Northern Lapwing adults and chicks was carried out in 2003. Five visits were made by volunteers across 14 sites in England and Wales (including Sites 1-4) during pre-defined three-week periods between mid-March and early July. The total number of adult Northern Lapwings and the number of adults alarming, or behaving as though they had young, were recorded and observations plotted on maps. Any chicks seen were recorded and the stage of development was assessed on a four-point scale (recently hatched; part grown; well feathered; fledged). All sites were undergoing intensive monitoring.

Chick body condition and survival

Chicks were ringed with a numbered metal ring when found in the nest within 24 hours of hatching. Body weight was measured to the nearest 0.5g using a 'Pesola' spring balance. Ringed chicks were relocated visually and recaptured whenever possible. Each time a chick was recaptured body mass was recorded as for newly-hatched chicks, as well as the location of the chick. Backpack mounted Holohill LB-2 or Biotrack 0.6g radio-tags were fitted to 52 newly-hatched chicks. 174 chicks were ringed in 2003, and 147 chicks were ringed in 2004. Only chicks on Sites 1 and 3 were tagged in 2003 (19 chicks) representing 14% of chicks known to have hatched on these two sites. In 2004 chicks on all four study sites were tagged (33 chicks) representing 18% of chicks known to have hatched. To avoid pseudoreplication, only one chick was tagged per brood. The weight of the tag represented 3.3% of the mean hatching weight of tagged chicks. The battery life of the tags was 21 days and they had a detectable range up to 1km, depending on the terrain. Chicks continued to be monitored until the end of the radio-tag battery life, the death of the chick or the loss of the signal from the radio-tag. The death of a tagged chick was confirmed either by recovering the tag or the carcass. In the cases where signals from radio-tagged chicks were lost, chicks were assumed to have died if the loss of the signal took place before with the end of the battery life. Regular signals were obtained from all tags prior to loss of signal.

Identification of the causes of chick mortality was based on the locations and conditions of recovery of the tag or chick carcass. In the case of radio-tagged chicks that disappeared (signal was lost and neither tag nor carcass was recovered) these chicks were assumed to have died. It was conceivable that some chicks were led out

of the detectable range of tags. However survival rates are known to be reduced the further a chick moves from its natal site (Galbraith 1988a), and regular checking for disappeared tags up to a week after disappearance through the entire study site and neighbouring fields reduced this possibility. None of the chicks declared dead were later found. Daily temperature and rainfall data from Ringway (52°21′N, 2°17′W) were obtained from the Meteorological Office, UK.

Statistical analyses

Average growth rate of chicks within this study was estimated by fitting Gompertz, von Bertelanffy, logistic and exponential equations to weight (in grams) and age (in days) of all chicks of a known age. The best fit was provided by the logistic curve ($y=a/(1+b\times\exp(-c\times age))$ where a is asymptotic mass, b is size at maximum growth (inflection point) and c is a growth rate constant.

An index of body condition was calculated as the difference between actual weight and that predicted by the logistic curve of weight against age, divided by the predicted weight. Generalized Linear Mixed Models implemented in SAS® v8.2 were used to investigate (i) egg volume (with normal error structure and identity link, with field and site as random terms to control for non-independence of nests within the same field and study sites); (ii) chick body condition with normal error structure and identity link, with field and site as random terms and chick identity, nested within brood, as a random term to control for repeated measures of chicks; (iii) daily mortality of radio-tagged chicks (with binomial error structure and logit link, with site as a random term and chick identity as a random term to control for repeated measures of chicks). Analysis of daily mortality was undertaken for the period from hatching up to 21 days of age, with data from chicks known to have died being included up to the age of death. Death was assumed to have occurred midway between the last observation of the chick and the visit on which death was confirmed.

In all GLMMs both backward and forward stepwise regression was undertaken to establish model robustness, and the terms were added to the model at $P < 0.1$ (forward regression) and omitted from the model at $P > 0.05$. Only significant terms remained

in the final minimal models. Two-way interactions terms were included in the modelling procedure.

In order to compare chick body condition with values reported from two other published studies (Redfern 1983; Beintema & Visser 1989b), we also calculated the residuals between measurements of chick mass obtained here, and the age-specific values expected from the published logistic (Redfern 1983) or Gompertz (Beintema & Visser 1989b) equations for Northern Lapwing chick growth. Residuals were then expressed as a proportion of the previously published value. This yielded two series of body condition indices: one expressed relative to the findings of Redfern (1983), and the other relative to Beintema & Visser (1989b). Both these studies found a poor fit of the growth curves to the raw body mass data for chicks less than five days old, so for chicks up to this age, comparisons have only been made where mean weights after hatching have been published.

Results

Growth rate

The logistic growth equation for the Northern Lapwing is Weight = 206.364/(1+11.540×exp(-0.094×age)), r = 0.939 (Fig 1). Mean weight at hatching was 17.7 ± 1.5g (S.D.) in comparison to 17.5 ± 1.9g (Beintema & Visser 1989b) and 18.2g (Redfern 1983). In the present study only one chick was observed at the point of fledging and it was known to have been 39 days old, which is almost the upper limit of the range of fledging period duration of 30-40 days, indicating a slow growth rate.

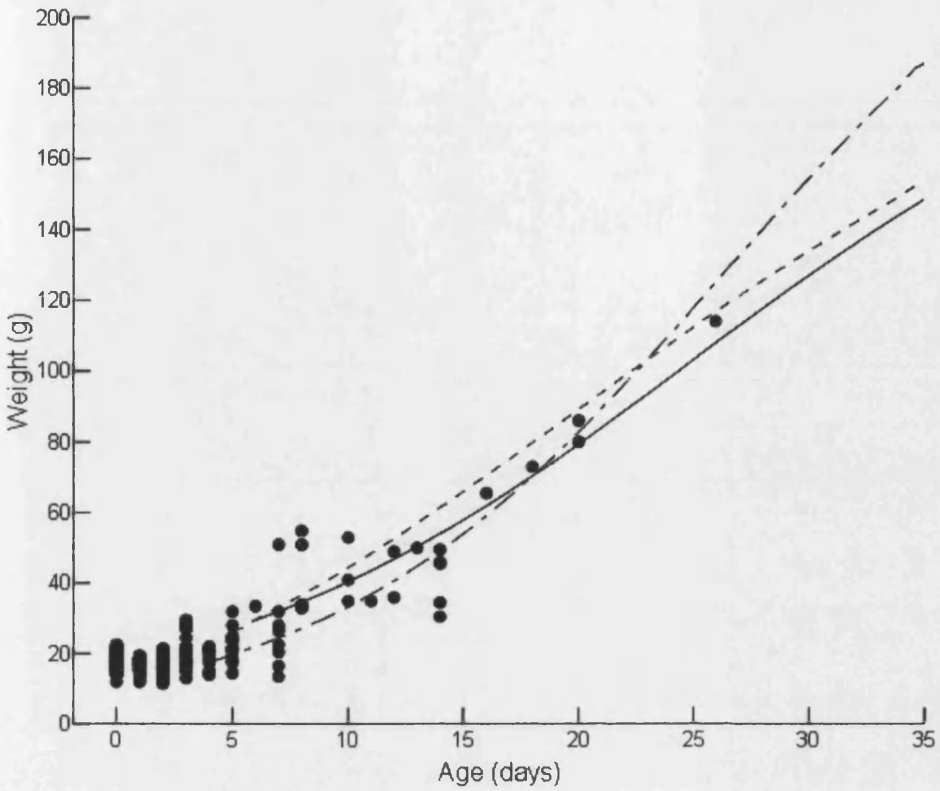

Figure 1. A comparison of Northern Lapwing chick growth between the present study (——, individual data points)) and previous studies by Beintema & Visser 1989b (----) and Redfern 1983 (- — -). Growth rate curves were fitted using logistic (Redfern 1983) and Gompertz (Beintema & Visser 1989b) equations.

Body condition

Body condition of chicks of all ages increased with mean egg volume of the clutch (GLMM: $F_{1,126} = 33.59$, $P < 0.0001$; Fig.2). In addition, there was significant variation in body condition among crop types (GLMM: $F_{6,126} = 2.95$, $P = 0.0099$).

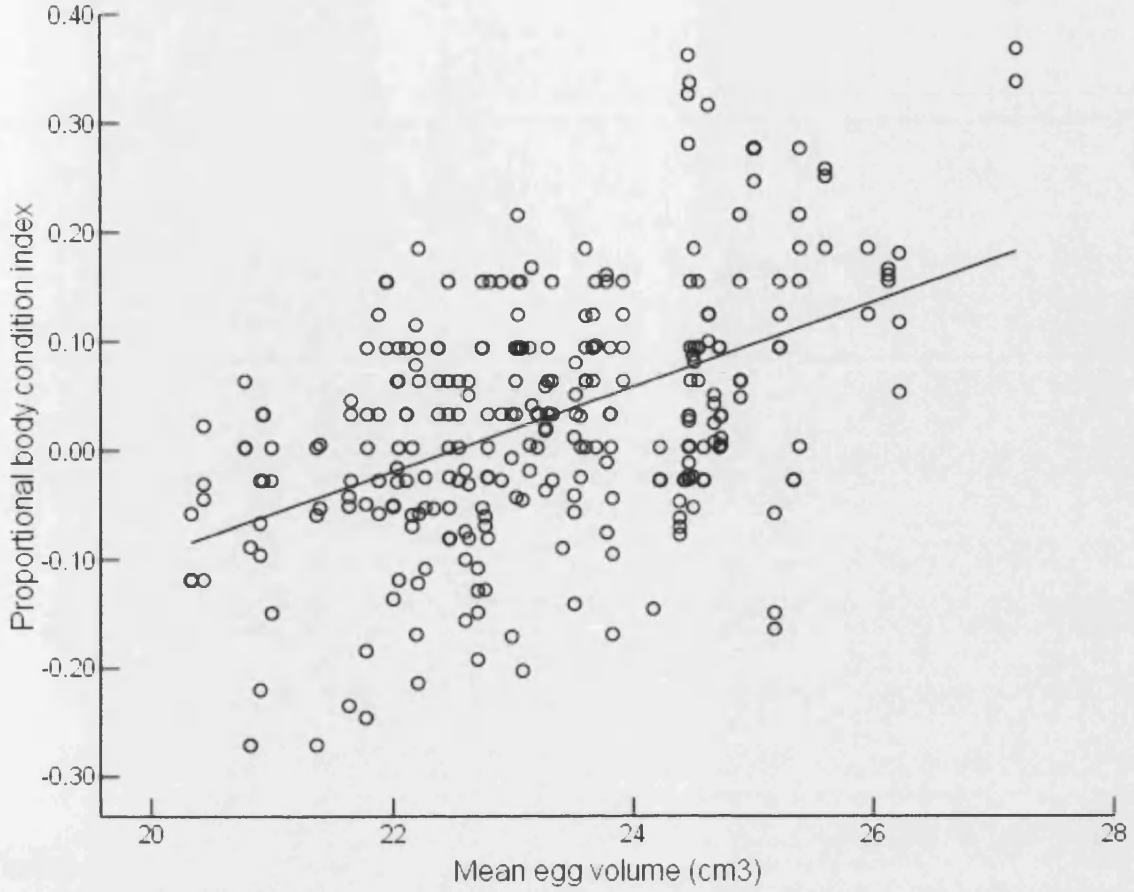

Figure 2. Relationship between body condition of chicks (mean) and mean egg volume (cm^3).

Egg volume, in turn, declined with egg laying date (GLMM: $F_{1,240} = 36.27$, $P < 0.0001$). This correlation was consistent across years and crop type (Fig.3).

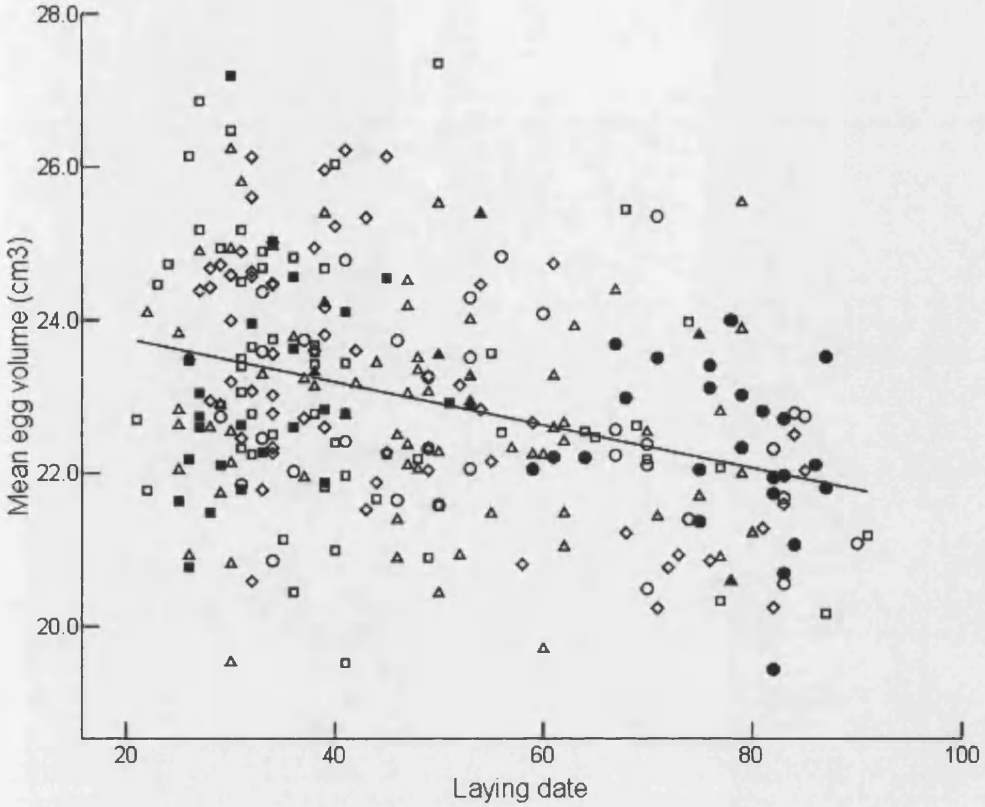

Figure 3. Relationship between laying date of first egg in clutch (days from March 1) and mean egg volume (n = 274 clutches). Crop types were winter cereal (■), rough grazing (○), maize (●), set-aside/over-winter stubbles (□), tillage (△), spring cereal (▲) and potatoes/onions (◊).

There was no significant variation in mean egg volume among years ($F_{1,240} < 0.001$, $P = 0.9801$), crop type ($F_{1,236} = 1.11$, $P=0.3592$), or clutch size ($F_{1,196} = 0.69$, $P = 0.4082$).

Chicks were in better condition if they were reared in spring cereal when compared to chicks reared in other crop types (Fig. 4). The movement of chicks among crop types was low: radio-tracking suggests that 88.7% of chicks remained in the same habitat in which they hatched. In total, only three radio-tagged chicks moved from their natal field to another field: two chicks moved from tillage to rough grazing, and one chick moved from spring cereal to rough grazing. Once the effect of egg volume was taken into account, there was no significant correlation between body condition and hatching date ($F_{1,127} = 0.02$, $P = 0.8958$), temperature ($F_{1,127} = 1.46$, $P = 0.2296$),

rainfall ($F_{1,127}$ = 0.68, P = 0.4120) or year ($F_{1,127}$ = 0.13, P=0.7232), or whether the chick was tagged with a radio-transmitter or not ($F_{1,127}$ = 0.51, P = 0.4780).

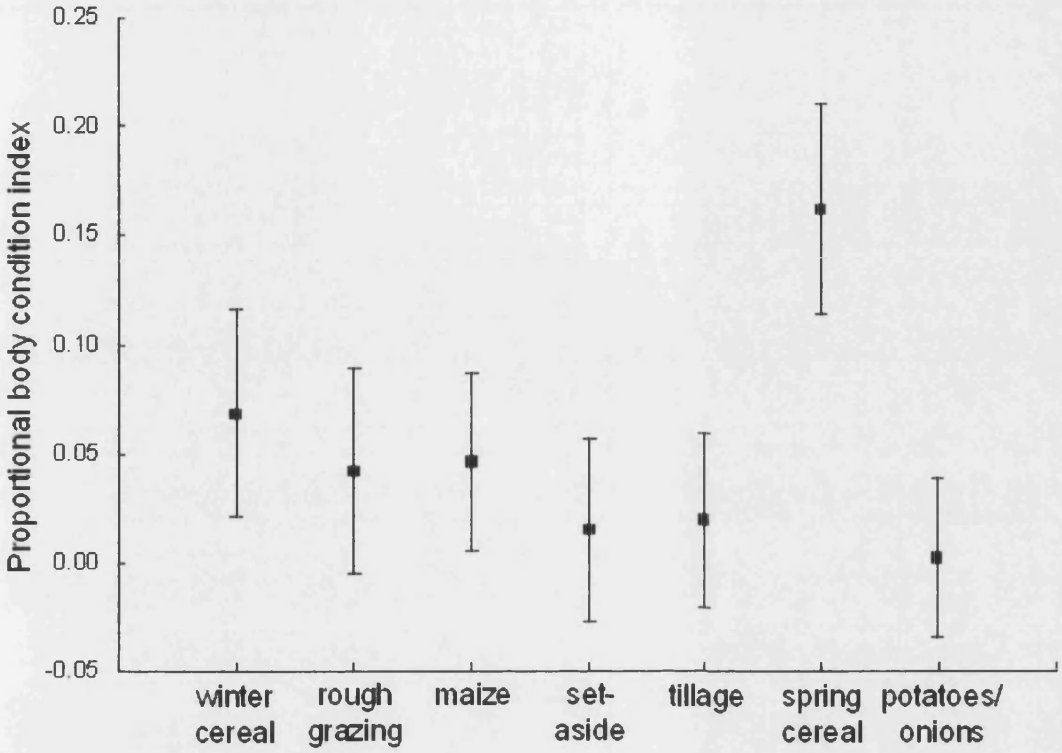

Figure 4. Model least squares mean body condition for chicks reared in different crop types (± S.E.). The model controls for the effect of egg volume on chick condition. Failure to account for this would lower the condition values for chicks hatching from small eggs laid later in the season (e.g. in maize crops).

A comparison of chick condition with previous studies showed that body condition indices were significantly below zero (comparison with Redfern (1983): 1-sample Wilcoxon W=3706, N=159, median=-0.05722, P<0.0001; comparison with Beintema & Visser (1989b): 1-sample Wilcoxon W=361, N=45, median=-0.0587, P=0.039) indicating that chicks from the present study were generally in poorer condition.

Chick survival

Radio-tagged chicks were recaptured every 1-4 days (2.7 ± 1.8 days). Of the 52 chicks fitted with radio-tags, only one survived the full 21-days of the tag's battery life, although it is not known whether this chick then survived to fledging. Of the remaining 51 chicks, 20 were taken by predators (tags or carcass were recovered), 27 chicks could not be located due to the absence of a radio signal and were assumed to

have been taken by predators and the tag damaged (the tags were not near the end of their battery life and all tags were functioning well prior to the loss of the signal). Three chicks were found with no signs of physical damage and we assume that they died from starvation or exposure, and one chick died from unknown causes but not predation. Of the 20 depredated chicks, one of the chicks was known to have been taken by a crow (crow was seen taking tagged chick and one untagged member of the same brood), one was taken by a fox (radio tag was found inside fox scat along with ring from another member of the same brood), one was taken by a mustelid (tag located in a hole in a ditch along with rings from the tagged chick and another brood member), and two were taken by raptors (tags recovered at base of pole with feathers on and around pole). The predator of 15 of the chicks was not identified (14 tags were recovered detached from chick but with feathers attached to tag and tag and/or aerial showing signs of damage and one tag was still attached to dead chick with right leg missing and leg and ring of another brood member found in vicinity.

In 49 out of 52 cases untagged members of the same brood were not seen alive beyond the known survival time of the tagged chick from the same brood. Out of the three cases when an untagged member of the brood survived the tagged member, only one chick was known to have fledged.

Overall breeding success was also assessed by recording the number of chicks seen in each weekly census up to August. Only one fledged juvenile each was recorded in both 2003 (a ringed chick but not tagged) in 2003, and 2004 (a chick neither ringed nor tagged).

The median survival time of radio-tagged chicks was 5.14 days (range 1-21 days; Fig. 5).

The low chick survival detected by radio-tracking is fully consistent with observations of volunteers. An analysis of the relationship between volunteer counts of fledged chicks (VCFC) and alarming adults (VCAA) and the number of fledged chicks (IMFC) as judged by intensive monitoring indicated a significant relationship according to the following equation: IMFC = 0.686 (SE=0.134) × VCAA + 1

(SE=0.264) × VCFC (R^2 = 0.771, $F_{2,12}$ = 20.25, P < 0.0001). The independent assessment of Northern Lapwing productivity on the present study sites in 2003 indicated that productivity was very low. No adults with young or any chicks were seen during the five visits to three of the sites and three adults with young were seen at the fourth site (although no adults with well grown or fledged chicks). The estimated number of fledged young as determined by the independent assessment is 2 (0.686 × 3 (number of alarming adults) + 1 × 0 (number of fledged young seen) = 2.058).

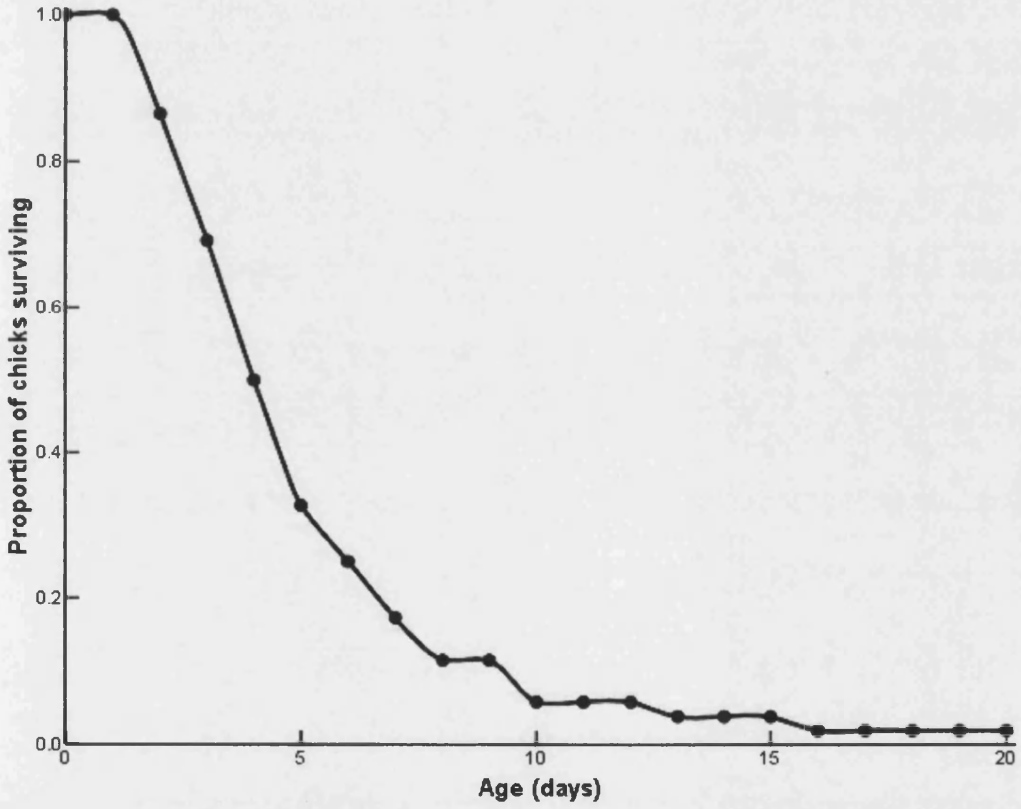

Figure 5. The proportion of radio-tagged chicks surviving up to the age of 20 days in North Wales 2003 and 2004.

Chick survival decreased with the age of the chick (GLMM: $F_{1,187}$ = 1159.9, P < 0.0001). There was also a significant positive correlation between mean body condition and daily mortality rate (GLMM: $F_{1,46.8}$ = 5.77, P = 0.0204). There was no relationship between daily mortality rates and hatching date ($F_{1,38.5}$ = 0.08, P=0.8518),

mean egg volume ($F_{1,228} = 0.60$, $P = 0.4388$), temperature ($F_{1,127} = 0.02$, $P = 0.8777$), rainfall ($F_{1,228} = 1.61$, $P = 0.2058$), crop type ($F_{6,92} = 0.42$, $P = 0.8717$) or territorial crow densities ($F_{1,228} = 1.82$, $P = 0.1781$).

Discussion

The first few days after hatching is a critical period for wader chicks. During this period their thermoregulatory capabilities are poorly developed and they must learn to feed themselves. The greatest mortality of chicks takes place during this critical period (Galbraith 1988c; Baines 1989; Grant 1991; Loegering & Fraser 1995; Grant *et al.* 1999). Northern Lapwings, in common with other waders, increase the chances of their chicks surviving this period by producing chicks with large yolk reserves. Chicks can survive on this yolk reserve for the first two to three days until they can feed themselves adequately. Large eggs produce large chicks which are likely to have larger yolk and/or protein reserves (Galbraith 1988c; Blomqvist *et al.* 1997) and which survive better than smaller chicks with smaller yolk reserves (Galbraith 1988b, Blomqvist *et al.* 1997). This study shows that early laid clutches comprise larger eggs, and that chicks hatching from large eggs are generally in better body condition than those from small eggs.

When and where chicks hatch and forage can influence body condition. Northern Lapwings rely on visual cues to detect prey and foraging efficiency (Butler & Gillings 2004; Devereux *et al.* 2004) declines with increasing vegetation height as prey-locating cues become less detectable and forager mobility is impeded. Autumn-sown crops and increased usage of fertilisers have led to increased sward growth and density during the breeding season, whereas spring-sown crops tend to have much shorter, less dense sward at the time when chicks are searching for food. In this study chicks reared in spring cereals were in better condition. However, although spring cereals have been shown to contain more surface and subsurface invertebrates than more intensively cultivated crops (Sheldon 2002), this crop type accounted for less than 2% of the available habitat and most chicks hatched on more intensively cultivated crops. Although there are potential benefits of hatching earlier in the season, from larger eggs and being raised on spring cereal crops, the overall condition of chicks was poor when compared to previous studies and the finding that condition

remained correlated with egg volume for all chick ages suggests that chicks did not live very long; that there was very little variation in food availability among sites and food availability was low.

Predation was the main cause of chick mortality in this study to the extent that only two fledged chicks (one ringed and one not ringed) were seen over the duration of the two-year study. Predation has been reported as a major cause of wader chick failure in other studies (Miller & Knopf 1993; Grant *et al.* 1999; Kruse *et al.* 2001; Hart *et al.* 2002; Sheldon 2002). All of these studies employed intensive monitoring similar to the present study and all (with the exception of the study by Hart *et al.* 2002) measured chick survival through the use of radio-tags. The assessment of chick survival in a precocial species is difficult without the aid of radio-tags or other means of tagging, especially in an agricultural environment where chicks are not easily spotted. The study by Grant *et al.* (1999) was conducted on Curlew chicks and a later analysis concluded that there were no detrimental effects of radio tagging on weight gain or chick survival (Grant 2002). Other studies on the effect of radio-tags on Wood Duck *Aix sponsa* duckling survival and body mass (Davis *et al.* 1999), Mallard *Anas platyrhynchos* ducklings thermoregulatory ability (Bakken *et al.* 1996) and Ring-necked Pheasant *Phasianus colchicus* chick survival (Kenward *et al.* 1993) all indicate that there are no negative effects associated with the radio-tagging of chicks. A comparison of the survival of radio-tagged chicks and non-tagged chicks from the present study suggests that chick survival is not affected by chicks being fitted with radio-tags. It is feasible that increased researcher activity at study sites may increase chick predation rates. However, as Northern Lapwing chicks are highly mobile and leave the nest scrape within hours of hatching, it is unlikely that a predator could determine the location of a brood by an earlier visit by a researcher. The identification of nest predators suggests that the main predators at these study sites were mammalian (see chapter 4) and not corvids which are more likely to locate nests or chicks by researcher activity. A study by Fletcher *et al.* (2005) found no evidence that the levels of experimental increase in disturbance reduced daily survival of clutches or increased daily clutch predation rates.

No previous studies of Northern Lapwing chick survival have reported such a low fledging rate or such high predation rates. Less than 1% of chicks were known to have

survived until fledging in comparison the findings of previous studies of 49-90% (Jackson & Jackson 1980), 25% (Galbraith 1988c), 15-43% (Baines 1990), 4-35% (Blomqvist *et al.* 1997), 25-70% (Parish *et al.* 2001), 10.6-14.5% (Sheldon 2002) and 4% (Hart *et al.* 2002) and 90.4% of radio-tagged chicks were lost to predators. A broad range of species prey on Northern Lapwing chicks as indicated by evidence from recovery of radio-tags and chick carcasses. Recent decades have seen a rapid increase in corvid numbers across the UK (Gregory & Marchant 1995; Baillie *et al.* 2005) as well as an increase in Sparrowhawks and Buzzards (Baillie *et al.* 2005). Corvid and raptor numbers are believed to have increased as a consequence of decreased control (Gregory & Marchant 1995) and the increase in raptors is also believed to be as a response to the release from the deleterious effects of organochlorine pesticides. Population trends in mammalian predator species have been more difficult to quantify. Evidence from game bags suggests that fox populations increased (Tapper 1992) possibly as a consequence of decreased keepering activity, and/or a response to the recovery of rabbit populations from myxomatosis. More recent estimates of fox densities presented by Webbon *et al.* (2004) appear comparable with Tapper (1992) suggesting that fox populations have remained stable in recent years.

Although many potential predator species are increasing in number, this study cannot critically assess whether high chick mortality rates are linked to increased predators nor identify to what extent different predator species are impacting on Northern Lapwing chicks.

Northern Lapwing declines are associated with agricultural intensification. The substantial loss of chicks to predators raises the question of whether land-use changes, habitat loss and habitat fragmentation have resulted in increased vulnerability of chicks to predation and that increased predation rates of chicks is preventing Northern Lapwing population recovery. The majority of chicks in this study were preyed upon within the first week after hatching. However, chicks that escaped predation during this first week were found to be in poorer condition and the growth rates of chicks were lower than those of previous studies suggesting that starvation through low food availability may be the ultimate cause of mortality beyond that crucial first week. As chicks get older their nutritional needs increase. If food availability is limiting chick

survival then we would predict a deterioration in survival and protracted development. Starvation probability is reduced by increasing daily food intake, but through being more active a forager spends a greater time exposed to predators. Thus, increasing food intake can increase the probability of predation (McNamara & Houston 1987; Cuthill & Houston 1997). There is a trade-off between the amount of time spent foraging and the amount of time spent on anti-predation behaviours. If the risk of predation is extremely high, then more time spent in anti-predation behaviour may result in less time spent foraging. This could lead to a potential loss in body condition leading ultimately to starvation. Alternatively, if food is a limited resource, then the need to spend more time foraging (or foraging in potentially more risky areas i.e. with less cover) may be putting chicks at higher risk of being taken by a predator. Hungry chicks may increase their mobility to try and locate food and thus increase their visibility to predators, leading to a reduction in survival rates, and chicks weakened by hunger may be less likely to respond appropriately to parental alarm calls, again leading to increased predation rates (Evans 2004). The surprising lack of chicks moving from fields in which they hatched combined with the relatively poor condition of most chicks suggests a lack of suitable foraging areas for chicks to move to, although in some cases at least, the predation pressure on chicks was so high that they were probably depredated before they were able to move in search of suitable foraging areas. A study of Curlew breeding success by Grant *et al.* (1999) suggested that although predation was the main proximate cause of breeding failure, land-use changes which could benefit generalist predator species or increase the vulnerability of nests to predation could be the ultimate cause of breeding failure. Similarly, our study suggests that although predation was the main cause of chick mortality, land-use changes leading to low food availability and increased vulnerability of Northern Lapwing chicks to predators are important factors influencing Northern Lapwing breeding failure.

Further research is needed to quantify the impacts of different predator species on chick survival. However, if attempts at reversing the decline of breeding Northern Lapwings on agricultural land in the UK are to succeed it is important to fully understand interactions between crop type, invertebrate abundance and chick growth. It is also imperative to quantify the impacts of different predator species on chick survival under varying conditions of invertebrate availability and integrate knowledge

of the behaviour and prey choice of generalist predators into future management plans.

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Chapter 6.

Does variation in demographic parameters account for regional variation in Northern Lapwing population declines across the United Kingdom?

Fiona Sharpe

Abstract

Over recent decades Northern Lapwing populations throughout the United Kingdom and Europe have declined in number and contracted in range size. Regional populations in the United Kingdom have declined at different rates with populations located towards the edge of the breeding range undergoing more substantial declines in breeding numbers. Nest monitoring data from the period of 1962 – 2003 were analysed to see if any differences in nest failure rates existed among regions. Estimates of nesting success were used in conjunction with aspects of Northern Lapwing dispersal extracted from ring recovery data to identify regional source and sink populations. Ring recovery data were also analysed to see if variation in regional population declines could be explained by variation in first-year and/or adult Northern Lapwing survival rates. There was no evidence to indicate the existence of source-sink dynamics at the regional level. Clutch failure rates have increased since the 1960s, and clutch failure rates were highest in grassland habitats. Clutch failure rates did vary among regions and regional increases in clutch failure rates were associated with an increasing proportion of birds nesting on grassland habitats. There was no association between regional clutch failure rates or adult and first-year survival rates and regional population declines. These results suggest that although recent increases in clutch failure rates may have influenced recent UK-wide population declines, it is not possible to explain variation in population decline among regions through source-sink dynamics, clutch failure rates or adult/first-year survival rates. It is more likely that chick mortality is the main determinant of poor Northern Lapwing productivity and population decline.

Introduction

Many wader species breeding in the United Kingdom (UK), such as Northern Lapwings *Vanellus vanellus*, Snipe *Gallinago gallinago*, Redshank *Tringa totanus*, and Curlews *Numenius arquata*, are currently undergoing widespread population declines (O'Brien & Smith 1992; Henderson *et al.* 2002; Wilson *et al.* 2005). Northern Lapwings are the most widespread and abundant of all wader species that breed in the UK. However, over recent decades there has been a marked decline in population size and a contraction in range size. Between 1987-1998 Northern Lapwings in England and Wales declined by 49% (Wilson *et al.* 2001), and between 1982-2002 Northern Lapwings breeding on lowland wet grassland in England and Wales declined by 36% (Wilson *et al.* 2005). Northern Lapwings have also declined in number in Scotland (Sim *et al.* 2005; Tayler & Grant 2005). Within the UK, the degree to which Northern Lapwings have declined has varied among regions (table 1). In general, populations found in more westerly regions (towards the edge of the European breeding range, Cramp & Simmons 1983) have undergone more substantial declines than populations situated further east.

Growing evidence exists linking Northern Lapwing population declines to changes in agricultural practices (see Beintema & Müskens 1987; Green 1988; Baines 1990; Berg 1992; Chamberlain *et al.* 2001; Wilson *et al.* 2001; Stephens *et al.* 2003). The direct impacts of modern agricultural practices have resulted in poor reproductive performance which is thought to be the main driving force of population changes in Northern Lapwings (Peach *et al.* 1994). Increasingly, predation of both eggs and chicks is seen as an important factor in determining reproductive success. An increase in nest failure rates during the 1990s has been ascribed to increased nest predation rates (Chamberlain & Crick 2003), and predation has been shown to be the main proximate cause of chick mortality (see Chapter 5).

Table 1. Regional population changes of Northern Lapwings breeding in the UK.

Region	*Population change (%) 1987-1998*[a]	*Population change (%) 1982-2002 (lowland wet grassland)*[b]
East Anglia	-53	-23
East Midlands	-59	-54
North England	-42	N/A
Northeast England	N/A	-38
Northwest England	-60	-30
Southeast England	-46	-30
Southwest England	-64	-62
Wales	-77	-69
West Midlands	-57	-58
Yorkshire/Humberside	-58	-30
Total for England & Wales	-49	-36
Scotland	-8[c]; -64 to -87[d]	N/A

[a] Wilson *et al.* 2001 ; [b] Wilson *et al.* 2005 ; [c] 1992 – 1997: O'Brien *et al.* 2002 ;
[d] upland habitat 1980/1991 – 2000/2002: Sim *et al.* 2005.

The level of any population can be determined by reproductive and mortality rates, as well as movements of individuals in and out of the population (Newton 1998). Previous work on Northern Lapwing survival rates have shown that there is no evidence to suggest that either first year or adult survival rates have declined sufficiently to have made a major contribution to the decline in the Northern Lapwing population at the UK level (Peach *et al.* 1994; Catchpole *et al.* 1999). In fact, over recent decades Northern Lapwing survival rates have increased implying that poor breeding success has been the most likely contributory factor to Northern Lapwing population decline (Peach *et al.* 1994).

Northern Lapwings tend to be highly philopatric, with both male and female adults exhibiting a high degree of breeding site faithfulness, and 60-70% of young returning to the natal or adjacent fields to breed (Thompson *et al.* 1994). A study by Thompson *et al.* (1994) on Northern Lapwing site-fidelity concluded that the stability of

Northern Lapwing populations is largely dependent on local breeding success (the number of birds produced locally) and, although immigration would not be sufficient to maintain stable population numbers, it could be important in the short term in bolstering declining populations.

One important aspect of Northern Lapwing population dynamics on which there are very limited data is the survival rates and fledging success of chicks. Because the Northern Lapwing is a precocial species assessing chick survival can be very time consuming and can only be done at a local level. Within the UK only a handful of studies have quantified chick survival and fledging success which ranged from <1% fledging success up to 90% (49-90%: Jackson & Jackson 1980; 25%: Galbraith 1988c; 15-43%: Baines 1990; 25-70%: Parish *et al.* 2001; 10.6-14.5%: Sheldon 2002; 4%: Hart *et al.* 2002; and <1%: see Chapter 4). However, because of the sparseness of the available data it is not possible to extrapolate these measures of chick survival and fledging success to the UK population as a whole.

Ecological data analyses are often carried out as separate studies of survival, fecundity and population size using different methods and datasets, which can result in the findings from such studies being difficult to compare with each other. Integrated analyses on Northern Lapwing datasets have been carried out in the past (Besbeas *et al.* 2002; Besbeas *et al.* 2005), however, there has not been any work carried out at the regional level nor any integrated work on dispersal.

The comparison of fecundity and survival rates and individual movements in the same population over a similar period can provide useful pointers to where the cause of the decline lie. The aim of this study is to bring together different datasets supplied by the British Trust for Ornithology (BTO) in an attempt to evaluate: (i) whether there is an existence of source-sink populations at the regional level within the UK Northern Lapwing population; and (ii) whether variations in natal philopatry, nest failure rates or first year and/or adult survival rates can account, to some extent, for regional variations in recent declines among the UK Northern Lapwing population.

Methods

Data

Nest success

The BTO Nest Record Scheme has been running since 1939. For the purpose of this chapter, only nest records from 1962 onwards were used. The Nest Record dataset includes information on the location of nests (county), nesting habitat, date of record, clutch size, estimate of clutch laying date, success or failure codes, and minimum and maximum exposure (in days). Nesting habitat was summarized into one of eight categories: arable, mixed grass/arable, wet grassland/marsh, pasture/rough grassland/improved grassland, heath/moorland, coastal habitat/saltmarsh, water and human/other. Nests were coded according to region (Scotland, North England, North-West, North-East, Wales, Midlands, East Anglia, South-East, and South-West).

Natal philopatry

The BTO has recorded ring recoveries of birds ringed in Britain and Northern Ireland since 1909. These data can provide useful information on Northern Lapwing dispersal from natal sites to breeding sites. Data were only used from Northern Lapwings ringed as chicks in England, Wales and Scotland, and then subsequently recovered dead during April and May i.e. the main breeding period in the UK (Cramp & Simmons 1983). Data were excluded when the date of death and/or place of recovery was not known with certainty. Data were also discarded if chicks had been held more than 24 hours prior to ringing, had been moved during ringing or if Northern Lapwings were recovered during the same breeding season as they were ringed. Variables included in the ringing dataset include the locations of ringing and recovery (county, latitude and longitude), year of ringing and recovery, distance moved between ringing and recovery (km) and direction moved (in degrees). Birds used in the analysis were allocated into one of seven regions in which they were ringed as chicks: Scotland, North England, North-West, North-East, Wales and South-West, Midlands, East Anglia and South-East.

Northern Lapwing survival

Northern Lapwing survival rates are derived from the BTO ring recoveries dataset. Only birds ringed as chicks and then subsequently recovered dead were included in

the analysis. Data were excluded if the birds were ringed as adults, held in captivity before or after ringing, and where there was uncertainty regarding estimated date of death or place of recovery. Years are measured from 1st May. To enable investigation of regional variations in survival, recoveries were placed into six regional categories (region 1: Scotland, region 2: North-West, region 3: North-East, region 4: Midlands, region 5: East Anglia and South-East, region 6: Wales and South-West). The analysis was then repeated with only three regional categories (region1: Scotland, region 2: North-West, Wales and South-West, region 3: North-East, Midlands, East Anglia and South-East). To investigate age-related survival rates recovered birds were coded as adults or first years (recovered within one year of ringing). As the exact age of chicks at the time of ringing was not known, the proportion of first years recovered pre- and post-fledging is not known with any certainty. Based on the assumption that Northern Lapwing chicks fledge between 29-42 days of age (Cramp & Simmons 1983), the proportion of first year birds recovered within 30 days of ringing (and therefore more likely to be pre-fledging birds) is 27% compared to 73% being recovered 31+ days after ringing (and most likely already fledged birds).

Data analysis

Nest survival

Daily clutch failure rates were analysed in SAS using a Generalised Linear Model employing an events/trial modelling approach with a binomial error structure and a logit link. Exposure days were calculated as the mid-point between minimum and maximum exposure days, provided values were no more than 10 days apart. Clutch failure rates were analysed in relation to year (linear and quadratic relationships), habitat, clutch laying date (linear and quadratic relationships), and region. Both backward and forward stepwise regressions were undertaken to establish model robustness and terms were added to the model at $P < 0.1$ (forward regression) and omitted from the model at $P > 0.05$. Only significant terms remained in the final minimal models. Two-way interactions terms were included in the modelling procedure.

Natal dispersal

General Linear Models (GLM) in SAS version 8.2 were used to investigate the relationship among explanatory variables and aspects of Northern Lapwing natal

dispersal. In the analysis of the proportion of birds dispersing from natal sites, in which the response variable was Northern Lapwing dispersal (0 = Northern Lapwing bred at natal site, 1 = Northern Lapwing moved 1 km or further from natal site to breed), the model employed a binomial error structure with a logit link and the number of birds ringed as chicks in each year as binomial denominator to control for temporal variations in ring reporting rates (as the population in the UK has grown the probability that rings are found and reported may have increased at different rates in different areas of the country). For analyses of dispersal distance and dispersal direction (in which the response variables were $\log_{10}$ distance (km) and direction (°) respectively), a normal error structure and identity link was used.

Northern Lapwing survival

Northern Lapwing survival was analysed using the program MARK. Because the number of birds marked was unknown, the BTO Ring Recovery option was used which assumed constant recovery rates among age classes and regions. Candidate models allowed for different survival rates between age classes (first year and adult). First year survival (x) was either constant (C) or time-dependent (T), as was adult survival (y). Candidate models also allowed for regional variations in either first year survival (C or T), adult survival (C or T) or both. The *a priori* set of candidate models were tested with the aim of selecting the 'best approximating model' (or small set of models) for statistical inference. Model selection was carried out using the AIC (Akaike 1973), where $AIC = -2 \ln(\mathcal{L}) + 2K$, where $\mathcal{L}$ is the model likelihood and K is the number of parameters. In order to account for model uncertainty, models were ranked according to the absolute value of the AIC, with the model with the smallest AIC being considered as the most plausible. Model selection was then based on the calculated AIC differences ($\Delta_i = AIC_i - AIC_{min}$) over all the candidate models in the set. Models with $\Delta_i \leq 2$ were considered as the best approximating models, and having substantial support as candidate models, given the data. The ratios of the Akaike weights (evidence ratios) comparing all models to the selected is the equivalent of judging the evidence by the relative likelihood of model pairs and is a useful tool for judging the evidence for the models being the best K-L (Kullback-Leibler) model in the set. The larger the evidence ratio between the best selected model and other models in the set the greater the evidence supporting the best selected model

(Burnham & Anderson 2002). Because the BTO model makes such strong assumptions about recovery rates to obtain survival estimates, it is not possible to really evaluate the fit of the global model (Gary White, pers. comm.).

Results

Nest survival

Between 1962 and 2003 the average proportion of nests surviving from laying to hatching assuming a 30 day incubation period was 61% (Mayfield estimate). Northern Lapwing daily nest failure rates did vary among different regions of the UK ($\chi^2_8 = 44.81$, $P < 0.0001$). The highest daily failure rates were in East Anglia and the North-East, and the lowest daily failure rates were in Wales and the South-West (Fig. 1).

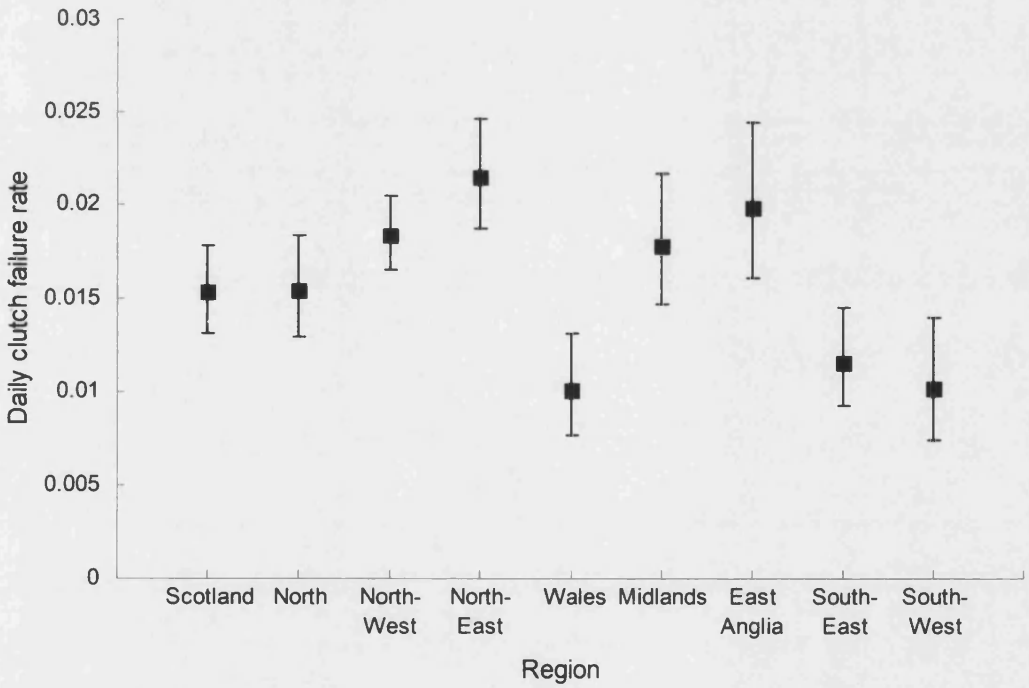

Figure. 1. Daily mortality rates of Northern Lapwing nests among different regions of the UK (mean ± 95% CL). For details of post hoc pairwise comparisons see appendix (pages i & ii).

Overall, daily failure rates increased between 1962 and 2003 ($\chi^2_1 = 6.88$, $P = 0.0087$). However, there were significant regional variations in daily clutch failure rate trends

($\chi^2_8 = 41.32$, $P < 0.0001$). Daily clutch failure rates increased over time in Scotland, North England and the South-East, with the most dramatic increase in East Anglia, but declined over time in the North-East, North-West, Wales, the South-West and the Midlands (Fig. 2). There was also a significant quadratic relationship between daily clutch failure rates and lay date ($\chi^2_1 = 62.83$, $P < 0.0001$). Daily failure rates of clutches also varied significantly between habitat (Fig. 3, $\chi^2_7 = 42.22$, $P < 0.0001$). Nests located in grassland habitats (wet grassland, pasture, heath/moorland and coastal/saltmarsh) had the highest rates of daily clutch mortality, whereas nests located in marginal habitats (water, human/other) had the lowest daily failure rates, and clutches located in arable and arable/mixed grass habitats had intermediate daily failure rates. The proportion of nest records submitted from grass-dominated habitats (wet grassland, pasture, heath/moorland and coastal/saltmarsh) compared to nest records submitted from arable or other dominated habitats (arable, mixed grass/arable, water and human/other) did change over time in different regions.

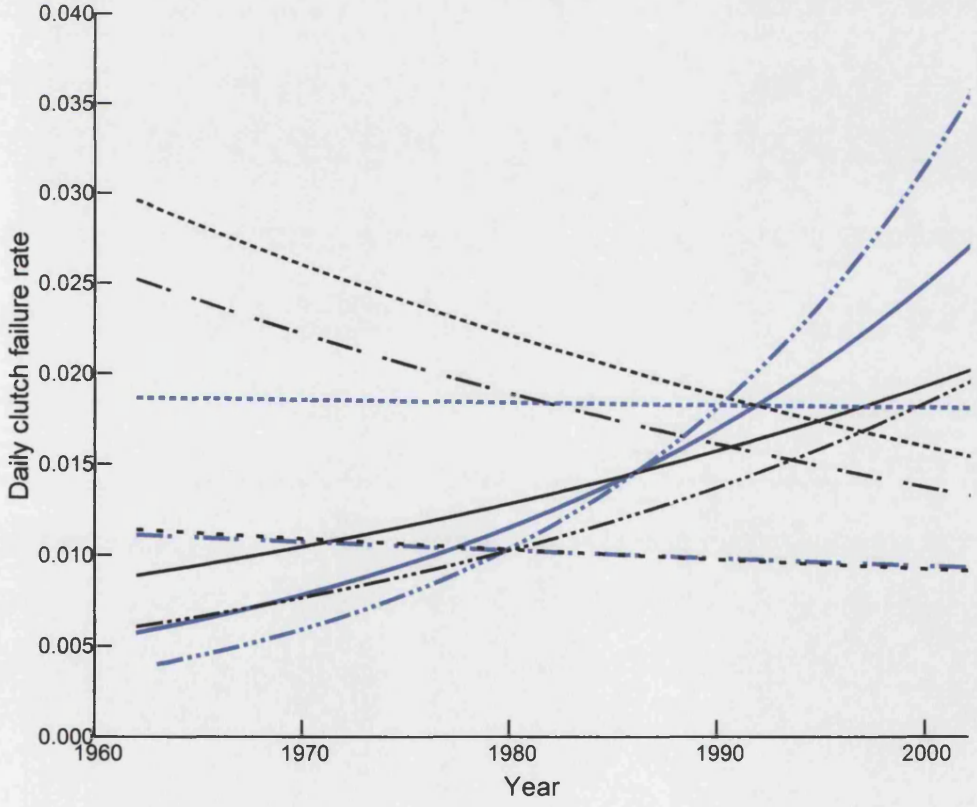

Figure 2. Temporal trends in daily clutch failure rates among different regions of the UK (model predicted values). Scotland —; North —; North-West -----; North-East -----; Wales - — - - — -; Midlands - — - - — -; East Anglia --- — ---; South-East --- — ---; South-West - - - -.

The proportion of nest records submitted from grasslands habitat increased over time in the North (Spearman rank correlation, r = 0.684, P < 0.001), East Anglia (r = 0.459, P = 0.006) and the South-East (r = 0.443, P = 0.005), but there was no change in the proportion of nest records submitted from grassland habitats in the seven remaining regions (Scotland: r = 0.029, P = 0.864; North-West: r = 0.069, P = 0.680; North-East: r = 0.021, P = 0.900; Wales: r = 0.156, P = 0.387; Midlands: r = 0.020, P = 0.909; South-West: r = 0.091, P = 0.593). For details of full and final model see appendix (page i).

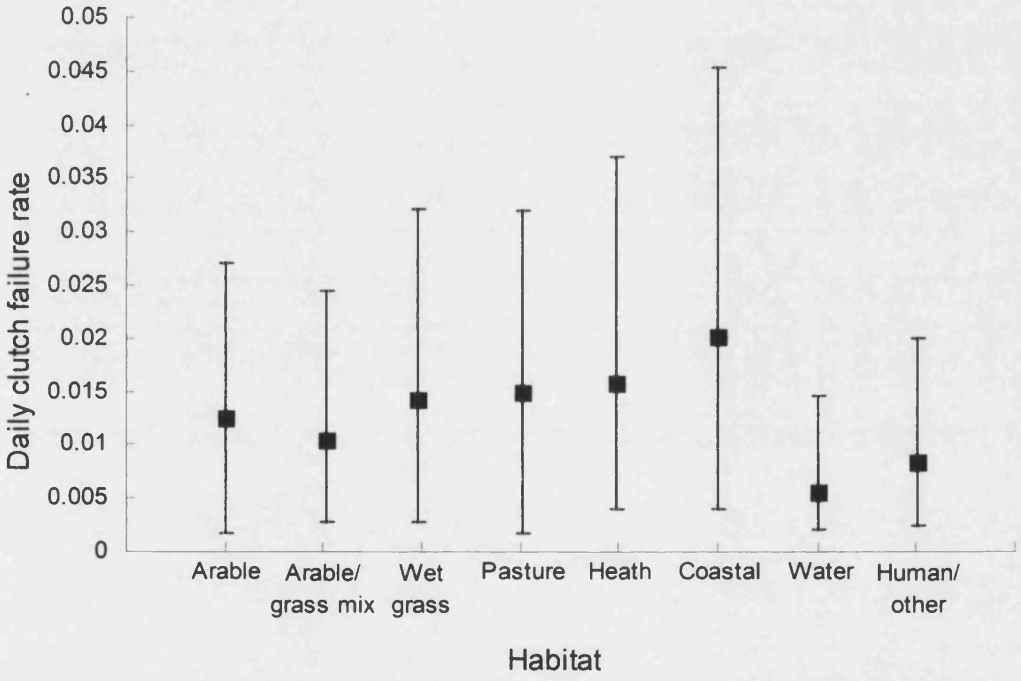

Figure 3. Figure. 1. Daily mortality rates of Northern Lapwing nests among different habitats in the UK (mean ± 95% CL). For details of post hoc pairwise comparisons see appendix (page ii).

Natal philopatry

Ring reporting rates have declined over time (1931 – 2000) (Spearman rank correlation, n = 69 r = -0.367, P = 0.002). This decline in reporting rate is due to a decline in the rate of reporting at ringing sites (n = 69, r = -0.500, P < 0.001) rather

than a decline in reporting rates of rings found away from ringing sites (n = 69, r = -0.017, P = 0.890).

An analysis of British ringing recoveries between 1931 and 2000 revealed that the proportion of birds dispersing from the natal site to breed has not significantly varied over time (GLM, χ^2_1 = 0.94, P = 0.3331). The proportion of birds exhibiting natal dispersal did not significantly differ among regions (GLM, χ^2_6 = 2.46, P = 0.8734) and there were no significant temporal variations in natal dispersal within regions (GLM, χ^2_6 = 6.11, P = 0.4109). There was no significant correlation between dispersal rates and latitude (χ^2_1 = 0.78, P = 0.3764) or longitude (χ^2_1 = 1.50, P = 0.2200).

The distance that dispersing Northern Lapwings moved between natal sites and new breeding sites significantly declined over time (Fig. 4, GLM, $F_{1,204}$ = 47.30, P < 0.0001) from 29.6 km (± 1.35 se) in the 1930's to 6.44 km (± 1.22 se) in the 1990's. Distance moved also varied significantly among regions (Fig. 5, GLM, $F_{6,204}$ = 3.82, P = 0.0012). See appendix for details of post hoc pairwise comparisons (page iii). There was no significant correlation between latitude ($F_{1,210}$ = 0.33, P = 0.5686), longitude ($F_{1,210}$ = 1.00, P = 0.3188) or direction ($F_{1,210}$ = 0.05, P = 0.8318).

There were no significant correlations between dispersal direction and year ($F_{1,210}$ = 0.81, P = 0.3685), region ($F_{6,205}$ = 0.33, P = 0.9233) or distance ($F_{1,210}$ = 0.58, P = 0.4487), latitude ($F_{1,210}$ = 0.03, P = 0.8681) or longitude ($F_{1,210}$ = 0.10, P = 0.9174).

The majority of birds that dispersed from their natal site remained within the same region to breed and only 13 out 220 birds changed region. There was no indication that Northern Lapwings dispersed to breed in new regions with lower nest failure rates (matched pairs t-test: mean natal region daily nest failure rate = 0.0144 ± 0.0009 se, mean breeding region daily nest failure rate = 0.0159 ± 0.0008 se, t_{13} = -1.039, P = 0.319). See appendix (pages iii, iv) for detail of full and final models.

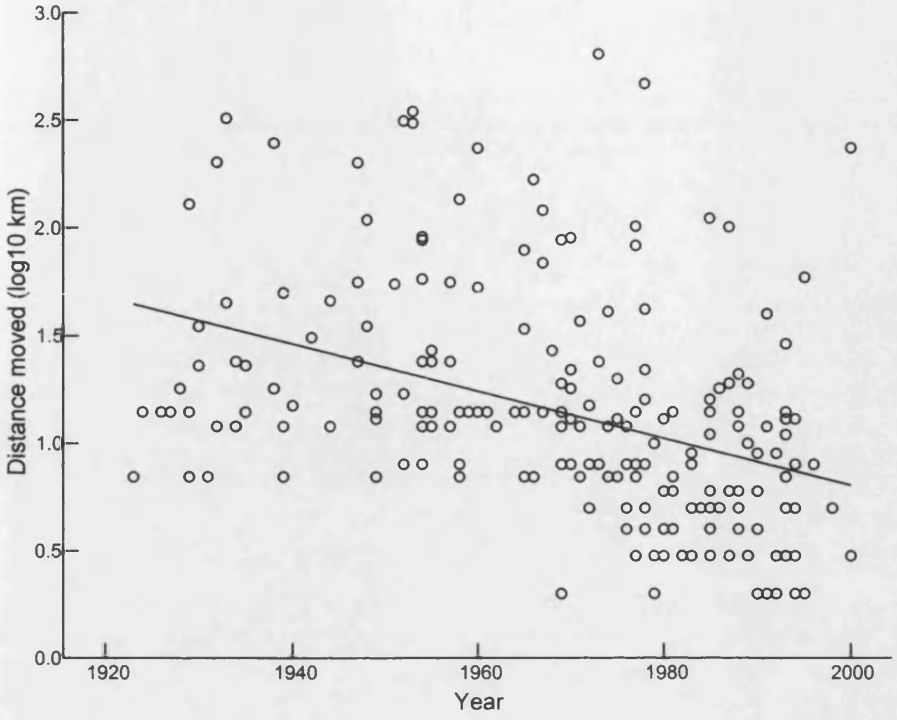

Figure 4. The distance that Northern Lapwings travelled from natal sites to new breeding sites from 1923 to 2000.

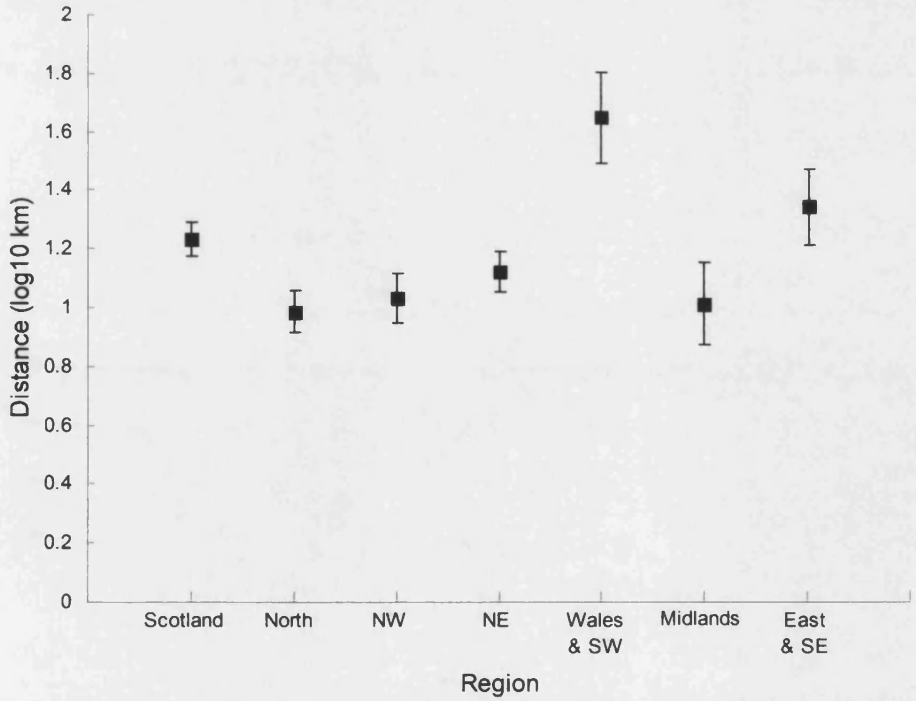

Figure 5. Regional variation in the distance that dispersing Northern Lapwings move from natal sites to breeding sites (mean ± 1se).

Northern Lapwing survival rates

The AIC values for candidate models are presented in table 2. The best approximating model (T/C) suggested there was a difference in survival between age classes, and that first year survival was constant over time (0.589 ± 0.017 se), whilst adult survival of 0.783 ± 0.0939 se was time dependent (Fig. 6). When ringing recoveries were divided into six regions within the UK, there was considerably less empirical support for regional variations in first year survival when compared to the best model. However, when ringing recoveries were placed into three regional categories, then there was substantial empirical support for regional variations in first year survival (Δ_i<2). Average first year survival rates were 0.557 ± 0.027 in Scotland, 0.628 ± 0.034 in the North-West, South-West and Wales, and 0.599 ± 0.026 in the North-East, Midlands, East Anglia and South-East. The evidence ratio for model C/T versus model C_{region}/T is only about 2 (w_1/w_2=1.91). This relatively weak for the best model suggests that we should expect to see a lot of variation in the selected best model from sample to sample if more data were available. There was essentially no support for regional variations in adult survival rates or time-dependent first year survival as indicated by the evidence ratios.

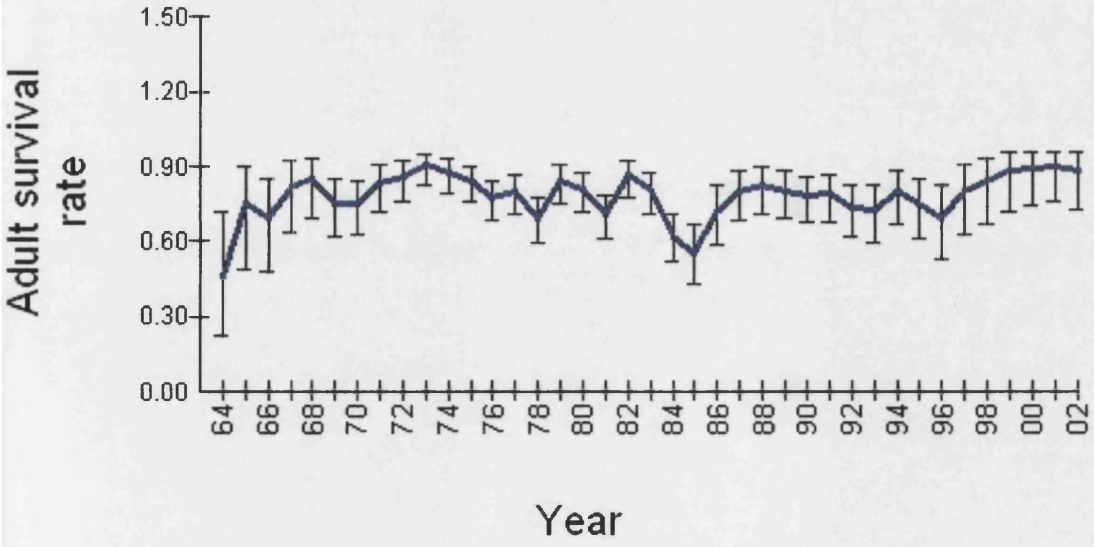

Figure 6. Estimates of adult Northern Lapwing survival rates (± 1 se) for the period 1963 to 2002.

Table 2. AIC values, Δ_i, Akaike weights (w_i) and evidence ratios for candidate models allowing for regional variations in first year and adult Northern Lapwing survival among six regions or three regions in the UK between 1963 to 2002. C denotes constant survival rates, T denotes time-dependent survival rates; x_{region} or y_{region} denotes when the candidate models allows for regional variations in survival rates.

Candidate models (x/y)	Three regional categories					Six regional categories				
	No. parameters	AIC	Δ_i	w_i	Evidence ratios	No. parameters	AIC	Δ_i	w_i	Evidence ratios
C/T	40	3869.79	0	0.655		40	3863.53	0	0.886	
C_{region}/T	42	3871.09	1.30	0.342	1.915	45	3867.89	4.36	0.099	8.949
C/C	2	3882.27	12.48	0.001	655	2	3872.20	8.67	0.012	73.83
C/C_{region}	4	3882.59	12.80	0.001	655	7	3878.60	15.07	0.001	866
C_{region}/C_{region}	6	3883.28	13.49	0.001	655	12	3882.16	18.63	0.000	-
C_{region}/C	4	3883.41	13.62	0.001	655	7	3875.97	12.44	0.002	-
T/T	77	3896.65	26.86	0.000	-	77	3888.49	24.96	0.000	-
T/C	40	3901.71	31.92	0.000	-	40	3889.92	26.39	0.000	-
T/C_{region}	42	3902.46	32.67	0.000	-	45	3897.38	33.85	0.000	-
C_{region}/T_{region}	120	3955.61	85.82	0.000	-	235	4125.64	262.1	0.000	-
C/T_{region}	118	3956.43	86.64	0.000	-	230	4115.36	251.8	0.000	-
T	39	3966.00	96.21	0.000	-	39	3957.99	94.46	0.000	-
T_{region}/C	115	3968.33	98.54	0.000	-	213	4119.22	255.7	0.000	-
T_{region}/C_{region}	117	3970.18	100.3	0.000	-	218	4132.08	268.6	0.000	-
T_{region}/T	152	3978.49	108.7	0.000	-	250	4160.08	296.6	0.000	-
T/T_{region}	156	4001.11	131.3	0.000	-	267	4188.22	324.7	0.000	-
C_{region}	3	4005.54	135.7	0.000	-	6	4006.76	143.2	0.000	-
C	1	4011.52	141.7	0.000	-	1	4008.15	144.6	0.000	-
T_{region}	117	4016.23	146.4	0.000	-	229	4169.16	305.6	0.000	-
T_{region}/T_{region}	228	4115.59	245.8	0.000	-	430	4759.54	896.0	0.000	-

Discussion

Movements of individuals within populations can facilitate rapid and localised changes in population densities and enable individuals to escape areas where survival or reproductive success are poor and to find other areas where conditions are better (Newton 1998). A source is an area where productivity is high enough to offset mortality, whereas the reverse is true for a sink (where mortality rates are higher than productivity rates). Therefore a sink population can only be maintained by a net import of individuals. If source-sink populations existed at the regional level within the UK population of Northern Lapwings, we would expect to see higher dispersal rates from regions of high productivity (measured as nest success) and relatively higher levels of immigration into regions with lower productivity. Although both nest survival rates and distances of natal dispersal were found to vary among different regions of the UK, there is no evidence to suggest that source-sink dynamics are operating at the regional level and it is highly unlikely that these factors could explain the variation in regional population declines over recent years.

Wales and the South-West have seen the greatest decline in breeding Northern Lapwings, yet these regions have the lowest nest failure rates in the country, in contrast to the North-East which has the lowest regional decline within England and Wales (Wilson *et al.* 2001) and yet had the highest nest failure rates of any region throughout the UK. In general, nest failure rates increased over time mainly in regions with lower rates of population decline (e.g. Scotland, North England, South-East) and declined in regions where population declines on the whole have been greater (e.g. Wales, South-West, North-West). A major change in agricultural practice which has been implicated in the decline in Northern Lapwing populations has been the reduction in the diversity of different types of agriculture per individual farm. This has resulted in the polarisation of arable and grassland with a concentration of arable land in eastern UK and pasture in western UK (Chamberlain *et al.* 2001). Nest failure rates are higher on grassland habitats and yet the two most westerly regions have the lowest overall nest failure rates. Although eastern parts of the UK are dominated by arable landscapes, the proportion of Northern Lapwings nesting on grassland habitats in these regions appears to have increased over recent decades. Although nest failure rates generally are lower on arable land, Northern Lapwings show a strong preference

for nesting on spring cereals (Wilson *et al.* 2001) and avoid nesting on autumn cereal crops. Another recent major change in agricultural practice has been the shift away from spring-sown crops to autumn-sown crops. This decrease in the availability of the preferred spring tillage may be resulting in greater proportions of birds nesting on the more unsuitable grassland habitats where nest failure rates are higher. Nests can fail to survive until hatching for various reasons, including predation, nest abandonment, trampling by livestock, destruction by farm machinery and infertile eggs (Chamberlain & Crick 2003; Trolliet 2003). However, a recent study by Chamberlain & Crick (2003) using the BTO's nest record cards suggested that the most common cause of recent nest failure was predation. The proportion of nests lost to predators was substantially higher in the 1990's than previous decades, and was high across all habitats, but especially in semi-natural and grassland habitats. Therefore, recent changes in the availability of suitable nesting habitats, resulting in a greater proportion of birds nesting on grassland habitats where nests appear to be more vulnerable to predation, may explain why nest failure rates have increased substantially in regions which so far have undergone slower rates of population decline.

All regional Northern Lapwing populations throughout the UK have declined in number, although to differing extents (Wilson *et al.* 2001; O'Brien *et al.* 2002; Sim *et al.* 2005). Recruitment in the Northern Lapwing is mainly driven by philopatry and hence, breeding success in a given area (Thompson *et al.* 1994). If local breeding success is poor, then immigration may be important in the short-term to bolster the population. Poor breeding success is the most likely contributory factor to recent population declines (Peach *et al.* 1994) and there is no evidence to suggest that immigration is occurring to any extent that would impact on population numbers. Therefore, the lack of dispersal among breeding Northern Lapwings within the UK and the lack of immigration from populations outside of the UK may have, to some extent, exacerbated recent population declines.

The estimate of adult and first-year survival rates of 0.783 and 0.589 respectively are similar to estimates from previous studies (0.60 first-year survival rate, 0.788 adult survival rate Peach *et al.* 1994; 0.828 adult survival rate Catchpole *et al.* 1999). One best approximating model (C_{region}/T) supported regional variation among first-year survival rates. Less than a quarter of first year birds were recovered within 30 days of

ringing suggesting that the estimated first-year survival rates are primarily post-fledging survival rates. Although regional variation in first-year survival may exist there is no association between lower first-year survival and greater population decline. The main reason for this investigation was to determine whether any regional variation in adult and/or first-year survival rates exist and whether regional survival rates could explain regional rates of population decline. The answer to this particular question is clear. Adult survival rates are constant among different regions within the UK, and regional variation in first-year survival rates does not correlate with regional population declines. First-year survival rates have remained constant with time, lending further evidence to the suggestion that changes in survival rates are not the cause of recent population declines. Peach *et al.* (1994) concluded that adult survival rates did not appear to have been responsible for the decline in the Northern Lapwings and that there was no evidence that first-year survival rates had declined sufficiently to have made a major contribution to the population decline in Northern Lapwings. Survival estimates from this analysis concur with the findings from the study by Peach *et al.* (1994).

Nest failure rates, especially failure due to predation, have increased over recent years, and may have influenced recent population changes. However, variation among recent regional population declines can not be explained by source-sink dynamics, nest failure rates or adult or first year survival rates. Northern Lapwing survival rates have increased over recent decades, and the average proportion of nest surviving until hatching of 61% is within the range of 35.4 – 76% estimated by previous studies (Trolliet 2003). It should be noted that these nest survival rates are taken from predominantly western European populations, and Northern Lapwing populations are undergoing widespread declines and range contractions across most of western Europe (Fuller *et al.* 1995, BirdLife International 2004). It is possible that increased clutch failure rates over recent decades have influenced Northern Lapwing productivity and therefore rates of Northern Lapwing population decline across the UK population as a whole, but nest failure rates can not explain variation in regional population declines. Northern Lapwing chick survival is the one aspect of reproductive performance on which very little data exist, yet it is more likely that chick mortality, rather than egg losses, is the main determinant of poor breeding success in many Northern Lapwing populations (Hudson *et al.* 1994; Trolliet 2003).

As predation rates on Northern Lapwing clutches have risen in recent years (Chamberlain & Crick 2003) it is likely that predation rates on chicks have also increased. The number of species that prey upon Northern Lapwing chicks is greater than the number of species that are known to take Northern Lapwing clutches (Trolliet 2003), yet no studies have so far attempted to assess the impact of different predator species on Northern Lapwing chick mortality or whether predation rates vary among different habitats. In order to understand factors influencing regional Northern Lapwing population declines, it is important that the role of chick mortality and its determinants are more fully understood.

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Appendix

Nest survival

Full model:

Effect	D.F.	Chi-square	P-value
Year	1	7.36	0.0067
Habitat	7	46.29	<0.0001
Lay date	1	61.94	<0.0001
Region	8	46.55	<0.0001
Lay date*region	8	16.61	0.0644
Year*region	8	42.72	<0.0001

Minimal model:

Effect	D.F.	Chi-square	P-value
Intercept	8	44.81	<0.0001
Region	1	6.88	0.0087
Year	7	42.22	<0.0001
Habitat	1	71.47	<0.0001
Lay date	1	62.83	<0.0001
Year*Region	8	41.32	<0.0001
Terms dropped		16.61	0.0644
Lay date*Region	8	17.79	0.0529

Post hoc pairwise comparison of clutch failure rates among different regions

Differences of Least Squares Means

Effect	Region	Region	Estimate	Standard Error	DF	Chi-Square	Pr > ChiSq
Region	1	3	0.1490	0.1596	1	0.87	0.3506
Region	1	4	-0.1285	0.1170	1	1.21	0.2721
Region	1	5	-0.4670	0.1258	1	13.77	0.0002
Region	1	6	0.4185	0.1750	1	5.72	0.0168
Region	1	7	-0.2970	0.1584	1	3.52	0.0607
Region	1	8	0.0140	0.2109	1	0.00	0.9471
Region	1	9	0.1665	0.1616	1	1.06	0.3030
Region	1	10	0.2641	0.2027	1	1.70	0.1926
Region	3	4	-0.2775	0.1423	1	3.80	0.0512
Region	3	5	-0.6160	0.1527	1	16.27	<.0001
Region	3	6	0.2695	0.1933	1	1.94	0.1634
Region	3	7	-0.4461	0.1798	1	6.15	0.0131
Region	3	8	-0.1350	0.2272	1	0.35	0.5524
Region	3	9	0.0175	0.1822	1	0.01	0.9236
Region	3	10	0.1151	0.2198	1	0.27	0.6005
Region	4	5	-0.3385	0.1055	1	10.29	0.0013
Region	4	6	0.5470	0.1591	1	11.82	0.0006
Region	4	7	-0.1686	0.1435	1	1.38	0.2402

Region	4	8	0.1425	0.2012	1	0.50	0.4788
Region	4	9	0.2950	0.1470	1	4.03	0.0448
Region	4	10	0.3926	0.1928	1	4.15	0.0417
Region	5	6	0.8855	0.1688	1	27.52	<.0001
Region	5	7	0.1700	0.1489	1	1.30	0.2536
Region	5	8	0.4810	0.2060	1	5.45	0.0196
Region	5	9	0.6335	0.1529	1	17.17	<.0001
Region	5	10	0.7311	0.1972	1	13.75	0.0002
Region	6	7	-0.7155	0.1960	1	13.33	0.0003
Region	6	8	-0.4045	0.2406	1	2.83	0.0927
Region	6	9	-0.2520	0.1983	1	1.61	0.2038
Region	6	10	-0.1544	0.2332	1	0.44	0.5080
Region	7	8	0.3110	0.2228	1	1.95	0.1627
Region	7	9	0.4635	0.1754	1	6.99	0.0082
Region	7	10	0.5612	0.2164	1	6.72	0.0095
Region	8	9	0.1525	0.2250	1	0.46	0.4980
Region	8	10	0.2501	0.2564	1	0.95	0.3293
Region	9	10	0.0976	0.2190	1	0.20	0.6558

Post hoc pairwise comparison of clutch failure rates among different habitats

Differences of Least Squares Means

Effect	habitat	habitat	Estimate	Standard Error	DF	Chi-Square	Pr > ChiSq
habitat	1	2	0.1914	0.1707	1	1.26	0.2619
habitat	1	3	-0.1309	0.1336	1	0.96	0.3274
habitat	1	4	-0.1798	0.0903	1	3.96	0.0466
habitat	1	5	-0.2323	0.1675	1	1.92	0.1654
habitat	1	6	-0.4807	0.1365	1	12.40	0.0004
habitat	1	7	0.8154	0.2523	1	10.44	0.0012
habitat	1	8	0.4234	0.1942	1	4.75	0.0293
habitat	2	3	-0.3223	0.1903	1	2.87	0.0904
habitat	2	4	-0.3712	0.1669	1	4.95	0.0261
habitat	2	5	-0.4237	0.2159	1	3.85	0.0497
habitat	2	6	-0.6721	0.1941	1	11.99	0.0005
habitat	2	7	0.6240	0.2838	1	4.83	0.0279
habitat	2	8	0.2320	0.2370	1	0.96	0.3277
habitat	3	4	-0.0489	0.1260	1	0.15	0.6978
habitat	3	5	-0.1014	0.1862	1	0.30	0.5860
habitat	3	6	-0.3498	0.1588	1	4.85	0.0276
habitat	3	7	0.9463	0.2681	1	12.46	0.0004
habitat	3	8	0.5543	0.2150	1	6.65	0.0099
habitat	4	5	-0.0525	0.1587	1	0.11	0.7409
habitat	4	6	-0.3009	0.1193	1	6.36	0.0117
habitat	4	7	0.9952	0.2512	1	15.70	<.0001
habitat	4	8	0.6032	0.1888	1	10.20	0.0014
habitat	5	6	-0.2484	0.1852	1	1.80	0.1798
habitat	5	7	1.0477	0.2870	1	13.33	0.0003
habitat	5	8	0.6557	0.2346	1	7.81	0.0052
habitat	6	7	1.2961	0.2715	1	22.79	<.0001
habitat	6	8	0.9041	0.2136	1	17.91	<.0001

Natal Philopatry

Natal dispersal rates

Full model:

Effect	D.F.	Chi-square	P-value
Year	1	2.75	0.0975
Region	6	1.82	0.1775
Latitude	1	0.14	0.7090
Longitude	1	1.34	0.2478
Year*Region	6	1.79	0.1808

Dispersal Distance

Full model:

Effect	D.F.	F statistic	P-value
Year	1	14.96	0.0001
Region	6	2.01	0.0662
Latitude	1	3.96	0.0479
Longitude	1	0.20	0.6527
Direction	1	0.29	0.5916
Year*Region	6	2.04	0.0622

Minimal model:

Effect	D.F.	F statistic	P-value
Year	1,204	47.30	<0.0001
Region	6,204	3.82	0.0012
Terms dropped			
Latitude	1,210	0.33	0.5686
Longitude	1,210	1.00	0.3188
Direction	1,210	0.05	0.8318
Year*Region			

Least Squares Means for effect region
Pr > |t| for H0: LSMean(i)=LSMean(j)

Dependent Variable: logdis

i/j	1	2	3	4	5	6	7
1		0.0087	0.0512	0.2242	0.0124	0.1521	0.4336
2	0.0087		0.6937	0.1763	0.0001	0.8665	0.0166
3	0.0512	0.6937		0.4030	0.0005	0.9176	0.0435
4	0.2242	0.1763	0.4030		0.0021	0.4890	0.1307
5	0.0124	0.0001	0.0005	0.0021		0.0026	0.1293
6	0.1521	0.8665	0.9176	0.4890	0.0026		0.0837
7	0.4336	0.0166	0.0435	0.1307	0.1293	0.0837	

Regions: 1=Scotland, 2=North England, 3=North-West, 4=North-East, 5=Wales & South-West, 6=Midlands, 7=East Anglia & South-East.

Dispersal Direction

Full model:

Effect	D.F.	F statistic	P-value
Region	6	0.96	0.4546
Year	1	2.56	0.1112
Latitude	1	1.69	0.1948
Longitude	1	0.15	0.6949
Distance	1	0.48	0.4903
Region*Year	6	0.97	0.4440